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## REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 7. REVISION OF *DIACODEXIS* (MAMMALIA, ARTIODACTYLA)

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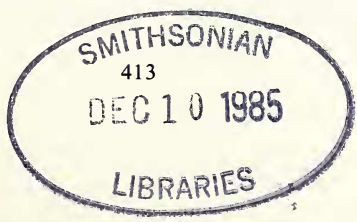
### ABSTRACT

Four species of *Diacodexis* occur in the early and middle Eocene of western North America—*D. secans* (including synonyms *D. laticuneus*, *D. olseni*, *D. metsiacus*, *D. brachystomus*) and new species *D. woltonensis*, *D. minutus*, and *D. gracilis*. *D. secans* is divided into four informal, temporally successive lineage segments (*D. s.-primus*, *D. s.-metsiacus*, *D. s.-kelleyi*, *D. s.-secans*) to reflect anagenetic change in derived morphologic features in this single evolutionary lineage and species from its Sandcouleean (earliest Wasatchian) through Blacksforkian (middle Bridgerian) occurrence. Other diacodexines and related groups arose from *D. secans* at different times in its anagenetic history—*D. gracilis* in the Graybullian from lineage segment *D. s.-metsiacus*; *D. woltonensis* and *D. minutus* in the Lysitean or Lostcabinian from *D. s.-kelleyi*; the *Wasatchia-Bunophorus* clade in the Sandcouleean from *D. s.-primus*; Leptochoeridae in the Gardnerbuttean (earliest Bridgerian) from *D. s.-secans*; and Antiacodontidae and Homacodontidae in the late Graybullian or early Lysitean from a *D. s.-metsiacus* sister group, Artiodactyla sp. A.

Evolutionary change (both anagenesis and cladogenesis) among these artiodactyls appears to have been gradual, chronoclineal, and mosaic, involving an increase in the degree

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of expression and frequency of occurrence of derived morphologic features, with canalization in single lineages and branching taxa. None of the apomorphic features are dichotomous; rather, they show normally distributed, continuous variation within species and overlap between species. Cladistic taxonomy cannot reflect such patterns. Different taxonomic treatments of anagenetic change within a single evolutionary lineage can result artificially in different apparent evolutionary patterns. Although the name *Diacodexis secans* represents "taxonomic stasis," it is emphatically not an indication of evolutionary stasis in the species *Diacodexis secans*. Similarly, neither the recognition nor naming of species different from *D. secans* implies a punctuated origin of or stasis in those species.

## INTRODUCTION

Artiodactyls are among the most common small and medium-sized fossil mammals in the early and middle Eocene of North America. Since their last major revision (Sinclair, 1914), new and much larger collections of these early artiodactyls have been recovered from Wasatchian through Bridgerian horizons in the western interior, including the Wind River Basin. The new material warrants and allows a complete reevaluation of the diversity, systematics and evolutionary relationships of early artiodactyls.

For example, study of the Wind River Formation artiodactyls indicates the occurrence of 13 species in seven genera—a much greater diversity of artiodactyls than hitherto recorded from the Wind River Formation or deposits of equivalent age. Of these taxa, three are new (two species of *Diacodexis*, one of *Homacodon*) and four represent new records for the Wind River Formation—*Hexacodus*, *Homacodon*, *Helohyus*, *Antiacodon pygmaeus*. The systematics and relationships of all North American species of *Diacodexis* are treated here. Other artiodactyl taxa—"D. *chacensis*," *Wasatchia*, *Bunophorus*, homacodontids, antiacodontids, leptchoerids—will be discussed elsewhere (Krishtalka and Stucky, manuscript; Stucky and Krishtalka, manuscript).

Eight North American species of *Diacodexis* have been named, all of which have had a tortuous taxonomic history. The type species, *D. laticuneus*, was originally referred to *Phenacodus* (Cope, 1882a) several months before Cope (1882b) named *Diacodexis*. The type specimen (AMNH 4202: P<sup>2-4</sup>, M<sup>1-3</sup>, M<sub>3</sub>) is a composite: the upper premolars (now apparently lost) belong to *Hyracotherium* and the upper molars to *Hyopsodus powellianus*; only the M<sub>3</sub> represents *D. laticuneus* (see Matthew, 1899; Sinclair, 1914).

*D. chacensis*, *D. secans*, *D. metsiacus*, and *D. nuptus* were originally identified as species of *Pantolestes* (Cope, 1875, 1881, 1882a) and later referred to *Trigonolestes* (Matthew, 1899) and *Diacodexis* (= *Trigonolestes*, Sinclair, 1914).

*D. brachystomus*, originally assigned to *Mioclaenus* (Cope, 1882a), was transferred to *Pantolestes* and then *Trigonolestes* by Cope (1884,



1894) and to *Diacodexis* by Sinclair (1914), who, in the same study, also named *D. olseni* and *D. robustus*.

Sinclair (1914) synonymized *D. brachystomus* and *D. metsiacus* with *D. chacensis*, an action later questioned by Gazin (1952). Guthrie (1967) referred *D. nuptus* to *Cynodontomys* and, following Gazin (1952), recognized *D. metsiacus* (including *D. brachystomus* and *D. laticuneus*), *D. chacensis*, *D. secans*, *D. robustus*, and, tentatively, *D. olseni* as valid species of *Diacodexis*. In 1971, Guthrie synonymized *D. olseni* with *D. secans*. In the midst of this taxonomic shuffling, two type specimens—those of *D. metsiacus* and *D. chacensis*—were apparently lost or mislaid.

In the Wind River Basin, the taxonomic history of *Diacodexis* begins with E. D. Cope's (1881) description of *Pantolestes secans* from the Wind River Formation. Later, Sinclair (1914) named *Diacodexis olseni* from a single lower jaw from Davis Ranch (=Sullivan Ranch; CM loc. 34), a locality in the upper part of the Lost Cabin Member, Wind River Formation; Van Houten (1945) added *Diacodexis chacensis* to the fauna from this member. White (1952) recorded *D. olseni* from Wind River deposits in the Boysen Reservoir area, and Kelley and Wood (1954) reported *D. chacensis* from the Lysite Member. Guthrie (1967, 1971) listed the presence of *D. metsiacus* in the Lysite Member and two species of *Diacodexis*, *D. metsiacus* and *D. secans* (including *D. olseni*), in the Lost Cabin Member.

Since 1971, field parties from the Carnegie Museum of Natural History and the University of Colorado have greatly increased the collection of artiodactyls from many localities in the Lysite and Lost Cabin members and Red Creek facies of the Wind River Formation. Most of these localities can be correlated lithostratigraphically and biostratigraphically; they range in age from the middle and late Wasatchian (Lysitean-Lostcabinian) to the earliest Bridgerian (Gardnerbuttean).

Our study of Eocene *Diacodexis* indicates that four species warrant recognition, of which three are new—*D. secans* (including *D. brachystomus*, *D. olseni*, *D. metsiacus*, and *D. laticuneus*) and new species *D. minutus*, *D. woltonensis*, and *D. gracilis*. A number of specimens assigned below to *Artiodactyla* sp. A and sp. B may eventually prove to represent a new species of *Diacodexis* or a new genus. In either case, they appear to be basal to the radiation of homacodontid and antiacodontid artiodactyls. *D. chacensis* is referred elsewhere to a new genus (Krishtalka and Stucky, manuscript), and *D. robustus* to *Wasatchia* (Stucky and Krishtalka, manuscript). *D. nuptus* is a species of *Arctodontomys*, a microsypid (Guthrie, 1967; Gunnell, 1985).

Among the four North American species of *Diacodexis*, *D. secans* is

by far the most common and longest lived, ranging from the Sandcouleean (earliest Wasatchian, 54.5 ma) to the Blacksforkian (middle Bridgerian, 50 ma) in the western interior. Its first occurrence, in part, marks the onset of the Wasatchian (Rose, 1981; West et al., in press). *D. woltonensis* is limited in known occurrence to the Lostcabinian of the Wind River Formation, Wyoming; *D. minutus* to the Lostcabinian and Gardnerbuttean of the Wind River Formation and the Lostcabinian of the Huerfano Formation, Colorado; *D. gracilis* to the late Graybullian of the Willwood Formation, Wyoming. *Artiodactyla* sp. A and sp. B occur in the late Graybullian and/or early Lysitean of Colorado (Debeque Formation) and New Mexico (San Jose Formation). Two species of *Diacodexis* have been reported from Europe (*D. gazini*, *D. varleti*; Sudre et al., 1983) and one from Asia (*D. pakistanensis*; Thewissen et al., 1983).

*Diacodexis*, specifically *D. secans* appears to be the most primitive known artiodactyl in dental morphology, and, as discussed below, is basal to the radiation of all other artiodactyls, a conclusion based on the range of morphological variation and anagenetic change in derived features in this Sandcouleean through Blacksforkian species-lineage.

One crucial point that has emerged from this study is the implication for systematics and evolutionary theory of variation within and among samples from single and disparate localities. In paleontological practice, morphology guides the allocation of specimens to individual species. But, the translation of the range and limits of variation into these paleontological species, either statistically or subjectively, can result in different reconstructions of evolutionary patterns. Very simply, taxonomic decisions regarding the composition of paleontological species can artificially determine the resultant evolutionary pattern and mode.

Recognition of paleontological species at a single locality and from a single horizon (lithosympatry; see Stucky, 1984) is usually straightforward: there is little or no morphological overlap between them, regardless of the number of species present, and each species exhibits a normally distributed variation.

However, complications arise when stratigraphically and geographically disjunct samples are added to the analysis and show varying degrees of morphological overlap in derived features with one or more species. Such diachronic or spatially separated samples are never morphologically congruent with one another to our knowledge. Grouping of these samples into paleontological species can involve several alternatives; it is especially difficult when the derived and overlapping features are not dichotomous, that is, not either present or absent, but merely evolving traits along several morphoclines.

This is exemplified by most samples of *Diacodexis*, which show a combination of continuous variation over geologic time and across

geographic space, with apparently continuous and directional change in the frequency and degree of expression of derived morphological features. Subdivision of such samples into a series of overlapping species (for example, Gingerich's 1976, 1979 treatment of notharctines)—to reflect this change as well as stratigraphic integrity—can imply a series of anagenetic speciation events. Alternatively, inclusion of such samples into one "evolutionary species" can *a priori* imply stasis and punctuationalism in some quarters (for example, Stanley, 1982, with regard to Schankler's, 1980, *D. metsiacus* in the Bighorn Basin). Clearly, in these instances, theoretical notions of evolutionary patterns can bias and determine taxonomic decisions; the reverse is also true—the composition and recognition of paleontological species can determine the evolutionary pattern.

The static and typological nature of Linnaean nomenclature when applied to a diachronic fossil record compounds this problem, especially when that record preserves temporally continuous morphologic change in derived features. Linnaean nomenclature cannot adequately reflect significant and continuous evolutionary change in a single lineage through time. Neither can cladograms. Cladistic conventions, which by definition are dichotomous, non-temporal and non-geographic, ignore this problem and assume that such anagenetic change is either minor, insignificant, or non-existent. However, a good fossil record, such as that of *Diacodexis*, flies major anagenetic change in the face of artificial conventions, as does a good Recent record of clinal change (Simpson, 1953; Gingerich, 1976, 1979; Wolpoff, 1985; Van Valen, 1982; Barnosky, 1982; Rose and Bown, 1984; Krishtalka and Stucky, 1983a, 1983b; Stucky and Krishtalka, 1983; Harris and White, 1979; Cooke, 1978; Endler, 1977; Rensch, 1960; Vrba, 1984; Chaline and Mein, 1979; Brunet and Heintz, 1982; Fahlbusch, 1983). Whatever the taxonomic solution adopted, the recognition and description of the pattern of morphologic variation through time and space, both within and among species, can untie this Gordian Knot and give a truer indication of evolutionary patterns than can ever be reflected by taxonomic nomenclature.

Our solution to the problem of translating anagenetic change in derived features in temporally disjunct samples (either stepped or continuous morphoclines; Endler, 1977) into taxonomic units is threefold: (1) We group such samples into one species, which is also an evolutionary lineage; such species-lineages are examples of anagenetic and phyletic evolution through time, with no increase in diversity. For this reason we choose not to divide such lineages into separate species. However, although the use of one species name to denote an evolutionary lineage may be "nomenclatorial stasis," it emphatically does not imply evolutionary stasis. Theoreticians who assay the fossil record



for patterns of stasis by simply counting numbers of named species and their geologic ranges (for example, Stanley, 1982) and disregard the morphologic patterns among and within these species are missing the evolutionary boat. This is not to say that stasis does not occur; it does, sometimes alongside gradualism (Krishtalka and Stucky, 1983a, 1983b; Williamson, 1981; West, 1979; Vrba, 1984).

(2) Evolving morphoclines (of especially non-meristic traits as well as size) are the hallmark of paleontological species-lineages. To reflect such change, we divide a species-lineage into *informal* lineage segments, which are temporally successive and morphologically overlapping units here designated by a hyphenated trinomial. Although the lineage segments and their names are informal, we follow nomenclatorial convention in using the available name of a synonymized species for a particular lineage segment if the type specimen of that species falls within the morphologic range of that lineage segment. For example, the species *Diacodexis secans* includes the informal lineage segments *D. s.-metsiacus* (contains cotype of *D. metsiacus* and holotype of *D. brachystomus*) and *D. s.-secans* (contains holotypes of *D. secans*, *D. olseni*, *D. laticuneus*), as well as *D. s.-primus* and *D. s.-kelleyi*, two new informal names. Obviously, assignment of individual specimens to particular lineage segments is based on relative position within the morphocline; but it is, in part, arbitrary, given the degree of morphologic overlap between temporally adjacent lineage segments. Clearly, a lineage segment cannot have invariant specializations that preclude its ancestral position with regard to descendant lineage segments. Lineage segments are, to us, preferable to "temporal subspecies." For one, subspecies are formal designations of spatial patterns within one species, whereas we intend lineage segments to be *informal* designations of specific temporal patterns within a species-lineage. For another, paleontological subspecies and the patterns they are invoked to reflect are usually ignored in the literature.

(3) We designate a diagnostic series of specimens (rather than one type specimen) to represent each lineage segment. This series encompasses the known range of variation and the degree of morphologic overlap with temporally adjacent lineage segments and other species. Holotypes represent formal taxa and, as such, do not apply to our informal lineage segments. Moreover, the use of holotypes detracts from the pattern of intrataxon variation by focusing attention on the morphological traits of a single specimen.

We recognize separate species (and cladogenetic events) where there is little or no morphologic overlap (in non-meristic traits and/or size) between geologically disjunct, penecontemporaneous, or lithosympatric samples, which themselves show continuous, normally distributed



variation. Recognition of separate species reflects cladogenetic events and an increase in diversity, but is not, in itself, evidence of a particular evolutionary tempo or mode.

Also, it is apparent that “paraphyletic” taxa, in the nomenclatorial sense, are real—different cladogenetic events can occur at different times from different lineage segments of an evolutionary species. For example, it appears that different taxa of artiodactyls—in hindsight, the most primitive members of originating suborders, families and subfamilies—arose at different times from different lineage segments of the single species *D. secans*. As such, some systematists would consider the genus *Diacodexis* and the species *D. secans* as “paraphyletic,” a label that may sacrifice evolutionary reality for classificatory and nomenclatorial convenience. The evolution of the *D. secans* lineage segment *D. s.-secans* and *D. woltonensis* from lineage segment *D. s.-kelleyi*, and the evolution of *D. gracilis* and *D. s.-kelleyi* from *D. s.-metsiacus* fall in the same category. These taxa may be “paraphyletic” according to cladistic convention, but they more nearly reflect the morphological and evolutionary pattern of species as reconstructed from the fossil record rather than does any scheme based solely on nomenclatorial conventions and dichotomous characters (Van Valen, 1978).

Finally, size is only *one* trait that figures in our recognition of some of the species of *Diacodexis*, as well as in the apparent pattern of anagenetic change in the species-lineage *D. secans*. Non-meristic morphological features are as or more important, and comprise most of the criteria in the diagnoses of species and lineage segments. As such, our evolutionary conclusions are based on suites of derived morphological traits, only one of which is size.

The presence and relative strength of three features used here—pseudohypocone, postmetacristid, talonid notch—are, along with others, of major importance in the systematics of *Diacodexis* and require precise definition. The pseudohypocone, on upper molars, occurs on the postprotocrista immediately posterior and adjacent to the apex of the protocone. The postmetacristid is a crest that descends the posterolingual face of the protoconid on  $P_4$  and that of the metaconid on the lower molars. The talonid notch occurs between the bases of the metaconid and entoconid on lower molars, where the talonid basin is deepest and opens lingually.

Abbreviations in text and tables are as follows: ACM, Amherst College Museum; AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; PU, Princeton University; UCM, University of Colorado Museum; USGS, United States Geological Survey, Denver; UW, University of Wyoming; L, length; W, width; N, number; C. V., coefficient of variation; SD, standard deviation.

## SYSTEMATICS

Family Diacodexidae (Gazin, 1955), new rank<sup>1</sup>

Subfamily Diacodexinae Gazin, 1955

*Diacodexis* Cope, 1882b*Diacodexis* Cope, 1882b:1029.*Trigonolestes* Cope, 1894:868.

*Type species.*—*Diacodexis secans* (Cope, 1881), including *D. laticuneus*, *D. brachystomus*, *D. metsiacus*, *D. olseni*.

*Included species.*—Type species and *D. minutus*, *D. woltonensis*, *D. gracilis*, *D. gazini*, *D. varleti*, *D. pakistanensis*.

*Known distribution.*—Early to middle Eocene of North America; early Eocene of Europe and Asia.

*Diacodexis secans* (Cope, 1881)*Pantolestes secans* Cope, 1881:187; 1884:725, plate 25a.*Pantolestes metsiacus* Cope, 1882a:149; 1884:719, plate 25e.*Phenacodus laticuneus* Cope, 1882a:181.*Mioclaenus brachystomus* Cope, 1882a:187.*Diacodexis laticuneus* (Cope, 1882a), Cope, 1882b:1029; 1884:492, plate 25e; Sinclair, 1914:290.*Pantolestes brachystomus* (Cope, 1882a), Cope, 1884:721, plate 23d.*Trigonolestes brachystomus* (Cope, 1882a), Cope, 1894:868; Matthew, 1899:34.*Hyopsodus laticuneus* (Cope, 1882a), Matthew, 1899:30, M<sub>3</sub> only.*Trigonolestes metsiacus* (Cope, 1882a), Matthew, 1899:34.*Trigonolestes secans* (Cope, 1881), Matthew, 1899:36.*Diacodexis chacensis* (Cope, 1875), Sinclair, 1914:290, in part; Kelley and Wood, 1954:364.*Diacodexis secans* (Cope, 1881), Sinclair, 1914:290; Guthrie, 1971:85.*Diacodexis olseni* Sinclair, 1914:292, fig. 26; White, 1952:202; Stucky, 1984:279.*Diacodexis metsiacus* (Cope, 1882a), McKenna, 1960:121; Guthrie, 1967:49; Delson, 1971:357; Rose, 1982:621.*Diacodexis* cf. *secans*, West, 1973:148.*Diacodexis* cf. *metsiacus*, Bown, 1979:106, fig. 59c-e.*Diacodexis* sp., Eaton, 1982:187, fig. 16E.

*Holotype.*—AMNH 4899, left and right P<sub>4</sub>–M<sub>3</sub>, from the Wind River Formation, Wind River Basin, Wyoming.

*Included lineage segments.*—*D. secans-primus*, *D. s.-metsiacus*, *D. s.-kelleyi*, *D. s.-secans*.

*Diagnosis.*—Larger than all penecontemporaneous species of *Diacodexis* and more robust than *D. gracilis*, *D. minutus* and *Artiodactyla* sp. A and sp. B, with more inflated molar protocones, metaconids and hypoconids. Additionally, differs from *D. gracilis* in having a less reduced and less medial paraconid on M<sub>1-3</sub>, and more nearly square

<sup>1</sup> *dexeos* is the genitive form of *dexis*; hence, Diacodexidae.

$M_{1-2}$ ;  $M_{1-3}$  talonids more shallow and cusps more bunodont than in *Artiodactyla* sp. A and sp. B and *D. minutus*;  $M_{1-3}$  metaconids less inflated in proportion to tooth size than in *D. woltonensis*;  $M_{1-3}$  paraconids and paracristids more developed than in *Artiodactyla* sp. A and sp. B, paraconids and metaconids less elevated, entoconid lower than hypoconid and hypoconulid not lingually placed near entoconid.

*Referred specimens and localities.*—See listing below under individual lineage segments.

*Known distribution.*—Earliest Wasatchian through middle Bridgerian (Sandcouleean through Blackforkian) of Wyoming and Colorado.

*Discussion.*—Our review of the types and other material of named species of *Diacodexis* indicates the following: (1) material from the early and middle Eocene previously identified as or allied to *D. secans*, *D. metsiacus*, *D. brachystomus*, *D. laticuneus*, *D. olseni*, and *D. chacensis* (in part) shows gradual temporal change with continuous overlap in the frequency and degree of expression of derived morphological features, as detailed below. This lineage represents a single evolutionary species, *D. secans*, which is a senior synonym of *D. metsiacus*, *D. brachystomus*, *D. laticuneus*, and *D. olseni*. Sinclair (1914), Gazin (1952), and Guthrie (1967, 1971) reached similar conclusions.

(2) *D. secans* is a Sandcouleean through Blackforkian evolutionary lineage in which we recognize four successive and informal lineage segments—*D. secans-primus* (Sandcouleean–early Graybullian), *D. s.-metsiacus* (late Graybullian), *D. s.-kelleyi* (Lysitean–?early Lostcabinian) and *D. s.-secans* (Lostcabinian–Blackforkian). Thus, *D. secans* includes Lysitean through Gardnerbuttean samples of *Diacodexis* from the Wind River Formation that were previously assigned to *D. secans*, *D. metsiacus*, and *D. olseni* (Sinclair, 1914; White, 1952; Guthrie, 1967, 1971; Stucky, 1982), as well as non-Wind River Formation material previously referred to or allied with *D. metsiacus* (McKenna, 1960; Delson, 1971; Bown, 1979; Rose, 1982), *D. secans* (West, 1973), and *D. chacensis* (Sinclair, 1914).

(3) *D. chacensis*, redefined on topotypic material, is referred elsewhere (Krishtalka and Stucky, manuscript) to a new genus.

(4) AMNH 17560, a lower jaw with  $P_4$ – $M_2$  from one of the Gardnerbuttean Huerfano localities, which was identified by Robinson (1966) as *Diacodexis* sp. cf. *D. secans*, bears the derived morphology of leptchoerids, and represents the earliest known occurrence of that family. This new genus and species will be described elsewhere.

Major anagenetic trends (or temporal morphoclines) between the successive lineage segments in this species involve: (1) increase in size, robusticity and bunodonty of  $P^2/2$ – $M^3/3$ ; (2) elongation of  $P^2/2$ – $P^4/4$  relative to the molars; (3) stronger protocone and metacone on  $P^3$ ; greater asymmetry of  $P^3$ , with protocone occurring more posteriorly;

development on  $P_4$  of a postmetacristid alongside the cristid obliqua; (4) development of a deep talonid notch and a strong postmetacristid on the lower molars; (5) inflation of molar metaconids, hypoconids, and protocones, with consequent weakening or obliteration of upper molar protocristae, conulecristae, and pseudohypocones; (6) some reduction and slight medial shift of the molar paraconid; (7) isolation of the hypoconulid on  $M_3$  and shortening of the hypoconulid lobe.

These trends appear to have evolved as a morphological nexus, with increasing canalization (by shifts in the frequency and degree of expression) and correlation of character states through time. For example, the postmetacristid and talonid notch on  $M_{1-3}$  are virtually absent in *D. s.-primus*, infrequent and weak (when present) in *D. s.-metsiacus*, more frequent and moderately developed (when present) in *D. s.-kelleyi*, and almost always present and strongly developed in *D. s.-secans*. Correlated with this temporal morphocline is the gradual increase in bunodonty (point 5 above) and the other trends cited above.

As such, there is significant and apparently continuous morphologic overlap between temporally adjacent segments of this lineage, with moderate shifts in the mean values and frequencies of character states. There is virtually no overlap between end members (*D. s.-primus*, *D. s.-secans*), which would be considered separate species if found in lithosympatry (they are not), and which indicates major anagenetic change rather than stasis. Each of the lineage segments, in turn, exhibits continuous variation in the character states listed above. Also, samples from discrete horizons, localities or stratigraphic intervals referred to each lineage segment show normally distributed patterns of variation. Individual specimens in zones of overlap cannot be assigned with confidence to one or another lineage segment. The same holds for isolated teeth, especially  $M_1$ s.

*D. secans* is the oldest known species of artiodactyl in North America and its first appearance, along with that of other genera, marks the onset of the Wasatchian (Rose, 1981; West et al., in press). It occurs penecontemporaneously with *D. gracilis* and *Artiodactyla* sp. A and sp. B (late Graybullian–early Lysitean), *D. woltonensis* (Lostcabinian), and *D. minutus* (Lostcabinian–Gardnerbuttean). As discussed elsewhere (Stucky and Krishtalka, manuscript), other diacodexoids (*Wasatchia*, *Bunophorus*), antiacodontids, homacodontids and leptochoebrids (*sensu stricto*, that is, *Leptochoerus*, *Stibarus*, *Ibarus*) appear to have arisen through cladogenesis from different lineage segments of *D. secans* and are most closely related to this species.

#### Lineage Segment *Diacodexis secans-secans* (Figs. 1–2; Tables 1–4)

*Diagnosis.* — Largest (mean size) and most robust lineage segment of *D. secans*, with  $P_2$  and  $P^{3/3}$  more elongate,  $P^3$  protocone more posterior,



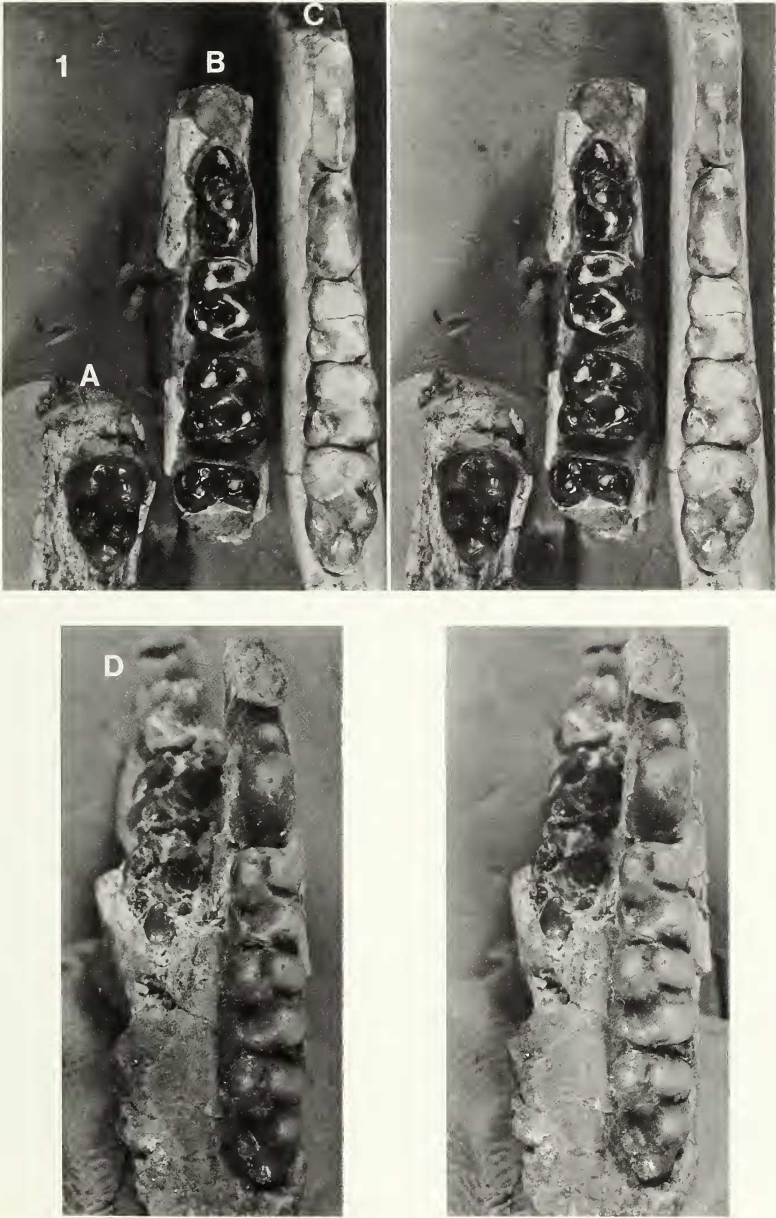


Fig. 1.—*Diacodexis secans* (lineage segment *D. s.-secans*). (A) AMNH 4202 (holotype of *D. laticuneus*); (B) AMNH 14937 (holotype of *D. olseni*); (C) UCM 42199; (D) AMNH 4899 (holotype of *D. secans*); all approx.  $\times 2$ .

$P_3$  longer than  $M_3$ , molars more bunodont,  $M_{1-2}$  more nearly square, more inflated molar protocones, conules, protoconids, metaconids and hypoconids, and less distinct protocristae, pseudohypocones and conulecristae;  $M_{1-3}$  with stronger postmetacristid and deeper talonid notch;  $P^4/4$ ,  $M^1/1$  proportionately broader and more robust.

*Diagnostic series.*—AMNH 4899 (holotype of *D. secans*), AMNH 4202 (holotype of *D. laticuneus*), AMNH 14937 (holotype of *D. olseni*); CM 42082, 43736, 22504, 22507, 43476, 35780, 21017, 22503, 44849, 39880, 43717; UCM 42199; PU 20599.

*Referred specimens.*—CM 21017, 21020, 21025, 21063, 21104, 21135–21138, 21140, 21213, 21217, 21228, 22503, 22504, 22506–22511, 22532, 27455, 27480, 30891, 30944–30948, 30950, 30951, 35732, 35771, 35772, 35774–35784, 35816, 36439, 36441, 36444, 36445, 36931, 36934, 37299, 37300, 37302, 37304, 37307, 37308, 40764, 40770, 40776, 40778–40781, 40784, 42073, 42074, 42079, 42080, 42082, 42087, 42096, 42097, 42125, 43469, 43475–43477, 43479, 43711, 43717, 43730–43737, 43744, 44846, 44849, 44908–44911, 51636, 55133, 55140, 55141, 55143, 55151, 55156, 55158, 55160, 55162, 55164–55169, 55351, 55353, 55356–55360, 55362, 55366, 55368; UCM 42199, 44906, 44341, 46508, 46582, 46809, 46811, 47026; AMNH 4202 (holotype of *D. laticuneus*), AMNH 14937 (holotype of *D. olseni*); PU 20598, 20599, 20800, 22317, 22471.

*Localities.*—CM locs. 91, 92, 99, 1039, 1040, 1041, 1042, 1046, 1077, 1084, 1534; PU loc. Alkali Creek (all Lostcabinian, Lost Cabin Mbr., Wind River Fm.). UCM locs. 80062, 81008 (Lostcabinian, Red Creek Facies, Wind River Fm.). CM loc. 216 (Lostcabinian, Wasatch Fm.). CM loc. 90 (Lostcabinian or Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.). CM locs. 34, 1036, 1038; UCM locs. 81010, 79041 (all Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.). CM loc. 1096 (Blacksforkian, Bridger Fm.); all in Wyoming.

*Known distribution.*—Late Wasatchian through earliest Bridgerian (Lostcabinian through Gardnerbuttean)—Wind River Basin (Wind River Fm.); late Wasatchian (Lysitean or Lostcabinian)—Bighorn Basin (?Willwood Fm.); late Wasatchian to middle Bridgerian (Lostcabinian—Blacksforkian)—Green River Basin (Wasatch Fm., Bridger Fm.); all in Wyoming.

*Description.*—Teeth anterior to  $P^2/2$  are unknown.  $P_2$  and  $P_3$  are elongate and narrow in occlusal view, and triangular in side view. The central, tall protoconid leans posteriorly and is joined by sharp cristids to a small anterobasal paraconid and a posterobasal cuspule (?hypoconulid). The roots of both premolars diverge ventrally.  $P_3$  is longer than  $P_2$  and has more nearly rectangular occlusal outline, a stronger paraconid and lower protoconid. The posterior crest (?cristid obliqua) to the posterobasal cuspule bears a hypoconid below the protoconid. A poorly developed cingulid rings the posterior one-quarter of the crown.  $P_3$  is longer than any of the other premolars and molars.

$P_4$  is shorter, wider and more robust than  $P_3$ , but is longer and as wide as  $M_1$ . In occlusal view it is rectangular to ovoid and wider posteriorly than anteriorly. The basal cingulid is well-developed except at the lingual and labial base of the protoconid. The anterobasal paraconid can be single or double. The cristid obliqua and hypoconid are variably developed but are always stronger than on  $P_3$ . On many  $P_4$ s a postmetacristid

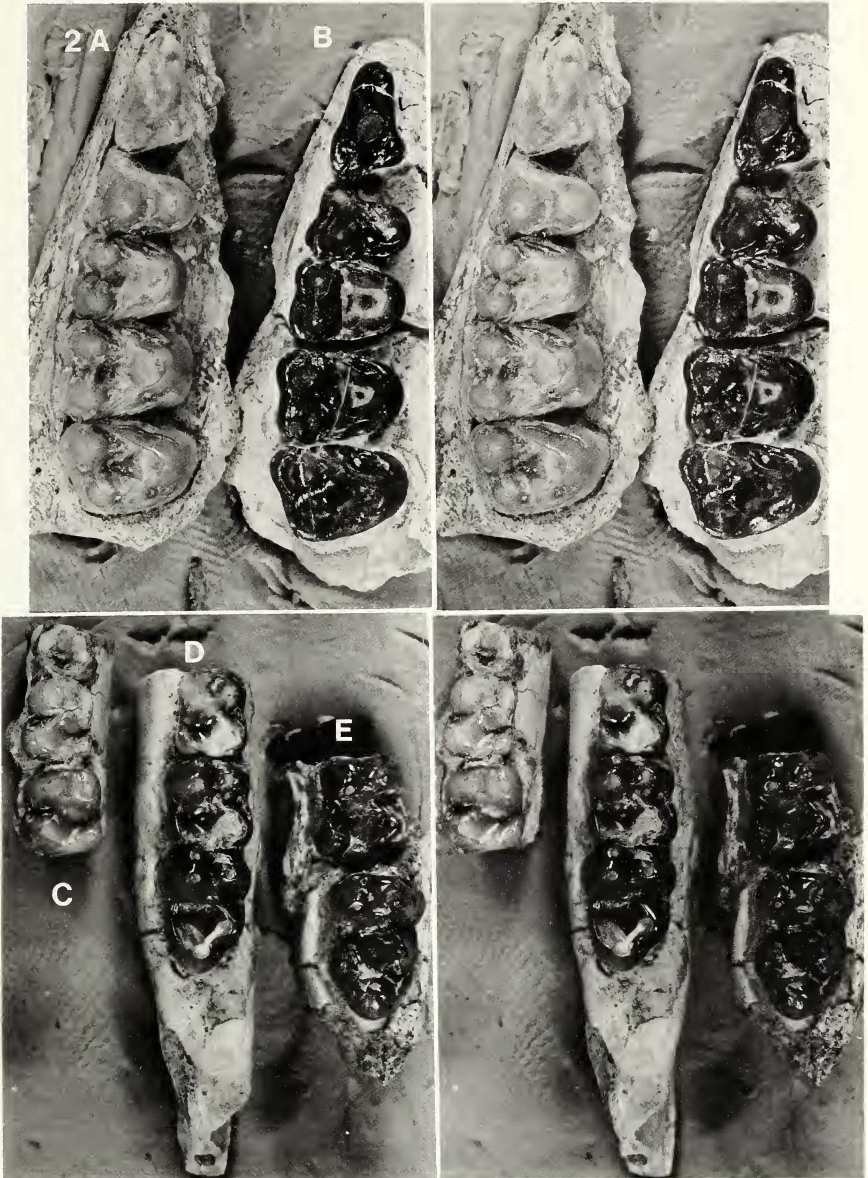


Fig. 2.—*Diacodexis secans* (lineage segment *D. s.-secans*). (A) and (D) CM 42082; (B) CM 43476; (C) CM 22504; (E) CM 21017; all approx.  $\times 2$ . (C), (D) and (E) show the range of variation in lower molars.



runs parallel and labial to the cristid obliqua from the protoconid to just above the talonid basin. Posteriorly, the basal cingulid may be crenulate, with several accessory cusps.

M<sub>1</sub> and especially M<sub>2</sub> are square in occlusal view, whereas M<sub>3</sub> is more rectangular and tapers posteriorly. The lower molars are robust and bunodont; all of the major cusps are inflated at the base. The metaconid is somewhat larger and taller than the protoconid and bulges lingually. The paraconid, much smaller than the metaconid, lies anterior and slightly labial to the latter. Both cusps are conjoined, so that only their apices are distinct. The cristid obliqua meets the trigonid medially or, especially on M<sub>1</sub>, just lingual to the mid-point. The hypoconid is larger and taller than the conical entoconid, which can be single, double or multicuspsate, especially on M<sub>3</sub>. The talonid basin opens lingually through a deep talonid notch, and a strong postmetacristid descends the posterolingual face of the metaconid to the notch. In some specimens the postmetacristid and pre-entocristid form a complete ridge that closes the talonid notch.

The talonids on M<sub>1-2</sub> are broader than or as wide as the trigonids, and slightly lower than the latter. The hypoconulid, smaller and lower than the entoconid, occurs just lingual to the midline of the crown; a strong notch separates the two cusps. A ridge-like postcingulid descends from the apex of the hypoconulid along the posterior face of the hypoconid. On M<sub>3</sub> the talonid is narrower than the trigonid, and the hypoconulid and hypoconid are equal in size and height.

P<sup>3</sup> resembles an asymmetrical triangle in occlusal view, and is almost twice as long as it is wide. The crown is dominated by a tall, central paracone. The preparacrista runs directly anteriorly and ends in a basal parastyle. The postparacrista runs directly posteriorly and bears a small, conical metacone. A weak protocone, the lowest of the cusps, occurs directly lingual to the notch between the paracone and metacone. As such, the protocone is offset posteriorly; its distance from the parastyle is twice that to the tip of the metastylar salient.

Unlike P<sup>3</sup>, P<sup>4</sup> and the upper molars are wider than long. P<sup>4</sup> bears a broad paracone labially, a smaller and lower protocone lingually, and a small parastylar wing. A strong cingulum runs around the base of the protocone.

M<sup>1-3</sup> are robust and bunodont, with basally inflated cusps, especially the protocone. M<sup>2</sup> is larger than M<sup>1</sup> and more nearly square; M<sup>3</sup> varies in shape from trapezoidal to triangular. On M<sup>1-2</sup> the paracone is slightly smaller than the metacone; both cusps are conical and joined by a shallow, anteroposteriorly directed centrocrista. The protocone is medial, and has a greatly expanded base, a long lingual slope, and a "pseudohypocone" bulge on its posterior face. Short protocristae extend to the metaconule and slightly smaller paraconule. Weak notches separate the conules from the protocone on some specimens. The external conulecristae are strong and reach the cingula, whereas the internal ones are either much weaker or virtually absent. The pre- and postcingula are broad and each bears a cuspule at a point adjacent to the labial face of the protocone. The ectocingulum is also well-developed and often crenulate. M<sup>3</sup> differs from M<sup>1-2</sup> in having a smaller metacone than paracone and, on some specimens, a weak, medial swelling (?mesostyle) on the centrocrista.

*Discussion.*—*D. s.-secans* is the end member of the evolutionary lineage (and species) *D. secans*. As described in the diagnosis, its diagnostic and derived morphologic features differ in frequency and degree of expression from those of the other lineage segments in the species, and are apparently the result of anagenetic evolution from the latter. *D. s.-secans* overlaps to a significant degree in size and most morphological features with *D. s.-kelleyi*, its immediate temporal predecessor, and less so with the other two lineage segments (Tables 1, 2).



In the Wind River Basin, *D. s.-secans* occurs in lithosympatry with *D. woltonensis* at Lostcabinian localities and with *D. minutus* at Lostcabinian and Gardnerbuttean ones (Figs. 12, 13). A single Gardnerbuttean horizon (at CM loc. 34) has yielded the largest sample of *D. s.-secans*, which shows a normal distribution that overlaps very little with that of the lithosympatric *D. minutus*. The two smallest specimens of *D. s.-secans* (CM 22504, UCM 46509) closely resemble the two largest of *D. minutus* (CM 40769, 42072) in size and degree of cusp inflation, but are distinct in the greater expansion of the posterior wall of the metaconid. Variable features in the CM loc. 34 sample of *D. s.-secans* include: size, strength, and position of molar paraconids; development of postmetacristids, talonid notches, conulecristae, cingula, and cingular cusps; strength and crenulation of the P<sub>4</sub> cingulid; presence of a P<sub>4</sub> postmetacristid. There is some morphologic overlap between a few specimens in this Gardnerbuttean sample (especially CM 22504) and Lostcabinian *D. woltonensis*, but there is no overlap between the latter and lithosympatric Lostcabinian samples of *D. s.-secans*.

*D. s.-secans* appears to be closely related to later leptocherids (Stucky and Krishtalka, manuscript), and may have shared an immediate common ancestry with *D. minutus* and *D. woltonensis*, a tentative conclusion based on their common possession of the following derived features—M<sub>1-3</sub> talonid short lingually; strong development of M<sub>1-3</sub> postmetacristid and talonid notch. However, given the variation in these features (absent to fully developed), as well as their occurrence in *D. s.-metsiacus* and *D. s.-kelleyi* (albeit at a weaker condition and lower frequency), they could have evolved in parallel in *D. minutus*, *D. woltonensis*, and *D. s.-secans*.

This lineage segment includes the type specimens of *D. secans* and junior synonyms *D. laticuneus* and *D. olseni*. Although the holotypes bear distinctive characteristics, these features vary greatly within Lostcabinian and Gardnerbuttean samples. The holotype of *D. secans* is perhaps unique in its combination of a large paraconid on P<sub>4</sub>, reduced molar paraconid, especially on M<sub>2</sub>, reduced entoconid on M<sub>1-3</sub>, and elongate hypoconulid lobe on M<sub>3</sub>. The left molars, recently prepared, have a stronger entoconid than the right ones. Nonetheless, all of these features occur on specimens previously identified as *D. olseni* and *D. secans* (Guthrie, 1971); the continuous variation within the latter includes the morphology of the type M<sub>3</sub> of *D. laticuneus*.

The holotype of *D. olseni* comes from CM loc. 34 (Gardnerbuttean), but the exact ages of the other two type specimens are uncertain. Judging from the fauna that was originally collected with the type of *D. secans* (Cope, 1881), its age is either Lostcabinian or Gardnerbuttean. The type M<sub>3</sub> of *D. laticuneus* is probably late Wasatchian, given that the

Table 1.—Summary statistics of lower dentitions of *Diacodexis secans* (lineage segments *Diacodexis secans-primus*, *D. secans-metstiacus*, *D. secans-kelleyi*, *D. secans-secans*), *D. woltonensis*, *D. minutus*, *D. gracilis*, and *Artiodactyla sp. A*.

Taxa and statistics	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
	L	W	L	W	L	W	L	W	L	W
<i>Diacodexis secans-secans</i>										
Range	6.0-7.3	2.0-2.7	5.2-6.2	2.5-3.4	4.0-5.3	3.2-4.1	4.3-5.3	3.9-5.3	5.6-7.1	3.7-4.9
N	6	6	20	20	39	41	53	54	47	52
Mean	6.53	2.32	5.62	3.00	4.53	3.64	4.79	4.41	6.36	4.35
SD	0.50	0.23	0.25	0.27	0.22	0.22	0.26	0.27	0.37	0.27
C.V.	7.66	9.91	4.45	9.00	4.86	6.04	5.43	6.12	5.82	6.21
Skewness	0.59	0.42	0.50	0.04	0.49	0.15	0.18	0.63	-0.22	0.12
<i>Diacodexis secans-kelleyi</i>										
Range	5.3-5.6	1.60	4.2-5.3	2.1-3.2	4.0-4.6	2.8-3.8	4.0-4.9	3.5-4.5	5.1-6.4	3.1-4.5
N	2	2	34	36	49	47	58	56	50	52
Mean	5.43	1.60	4.80	2.61	4.25	3.31	4.47	3.97	5.73	3.72
SD	—	—	0.30	0.22	0.16	0.22	0.23	0.26	0.30	0.26
C.V.	—	—	6.25	8.43	3.76	6.65	5.15	6.55	5.24	6.99
Skewness	—	—	0.01	0.27	0.43	-0.03	0.02	-0.01	-0.09	0.30
<i>Diacodexis secans-metstiacus</i>										
Range	5.0-5.8	2.0-2.2	4.5-5.7	2.2-3.6	3.7-4.6	3.0-3.6	4.0-4.7	3.3-4.2	4.6-5.8	3.1-4.0
N	5	4	28	29	32	39	50	52	34	38
Mean	5.54	2.10	4.95	2.79	4.16	3.27	4.36	3.73	5.17	3.43
SD	0.33	0.12	0.28	0.33	0.16	0.17	0.19	0.24	0.28	0.21
C.V.	5.96	5.71	5.66	11.83	3.85	5.60	4.36	6.43	5.42	6.99
Skewness	-0.96	—	0.45	1.00	-0.23	0.08	-0.15	-0.04	-0.02	0.23
<i>Diacodexis secans-primus</i>										
Range	4.7-5.0	1.7-2.0	4.2-5.0	2.1-2.9	3.8-4.3	2.9-3.4	4.0-5.0	3.5-4.2	5.0-6.7	3.5-4.1
N	4	5	18	19	20	25	40	41	39	39
Mean	4.85	1.84	4.61	2.46	4.07	3.17	4.51	3.89	5.83	3.75
SD	0.13	0.03	0.25	0.22	0.13	0.16	0.22	0.17	0.36	0.20
C.V.	2.68	7.07	5.42	8.94	3.19	5.05	4.88	4.37	6.17	5.33
Skewness	—	-1.1	0.08	0.36	-0.16	-0.24	0.05	-0.14	0.30	0.20

Table 1.—Continued.

Taxa and statistics	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
	L	W	L	W	L	W	L	W	L	W
<i>Diacodexis woltonensis</i>										
Range	2.40		5.0-5.7	2.6-3.1	4.0-4.3	3.2-3.4	4.1-4.3	3.5-4.0	4.9-5.6	3.4-4.0
N	1		6	6	5	5	7	7	7	7
Mean	2.40		5.35	2.83	4.14	3.32	4.21	3.76	5.27	3.70
SD	—		0.27	0.22	0.13	0.08	0.07	0.16	0.26	0.23
C.V.	—		5.05	7.77	3.14	2.41	1.66	4.26	4.93	6.22
Skewness	—		-1.0	0.44	-1.1	-0.34	-1.3	-0.1	0.15	-0.26
<i>Diacodexis minutus</i>										
Range	5.0-5.4	1.7-2.0	4.1-5.0	2.0-2.8	3.6-4.4	2.6-3.5	3.7-4.4	3.1-3.6	4.5-5.4	2.9-3.6
N	3	3	23	23	27	27	34	34	26	27
Mean	5.20	1.83	4.56	2.47	3.85	3.06	4.02	3.40	4.82	3.22
SD	0.20	0.15	0.24	0.21	0.17	0.18	0.19	0.14	0.19	0.17
C.V.	3.85	8.20	5.26	8.50	4.42	5.88	4.73	4.12	3.94	5.28
Skewness	—	—	-0.49	-0.52	1.29	0.01	0.27	-0.54	0.76	0.50
<i>Diacodexis gracilis</i>										
Range			3.9-4.0	2.2-2.3	3.7-3.8	2.8	3.7-3.9	3.3-3.8	4.5-4.8	3.00
N			2	2	3	3	3	3	2	2
Mean			3.95	2.25	3.77	2.80	3.83	3.47	4.65	3.00
SD			—	—	0.06	—	0.12	0.29	—	—
C.V.			—	—	1.59	—	3.13	8.36	—	—
<i>Artiodactyla</i> sp. A.										
Range	1.50		4.1-4.9	2.1-2.3	3.7-4.2	2.7-2.9	4.0-4.3	3.2-3.6	4.7-5.2	2.8-3.3
N	1		3	3	2	5	7	8	9	9
Mean	1.50		4.50	2.17	3.95	2.80	4.14	3.39	4.97	3.09
SD	—		0.40	0.12	—	0.07	0.11	0.15	0.18	0.15
C.V.	—		8.89	5.53	—	2.50	2.66	3.54	3.62	4.85
Skewness	—		—	—	—	0.00	-1.8	0.24	-0.2	-0.68

Table 2.—Summary statistics of upper dentitions of *Diacodexis secans* (*lineage segments Diacodexis secans-primus*, *D. secans-metsiacus*, *D. secans-kellelyi*, *D. secans-secans*), *D. minutus*, *D. gracilis*, and *Aritodactyl sp. A*.

Taxa and statistics	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
	L	W	L	W	L	W	L	W	L	W
<i>Diacodexis secans-secans</i>										
Range	5.6-6.0	3.7-4.0	4.0-4.3	4.7-5.8	4.0-4.8	5.3-6.9	4.5-5.5	5.9-7.3	4.4-5.0	6.0-7.0
N	2	2	6	7	19	19	26	26	17	18
Mean	5.80	3.85	4.13	5.14	5.70	4.37	4.88	6.59	4.71	6.44
SD	—	—	0.14	0.37	0.18	0.25	0.29	0.38	0.22	0.38
C.V.	—	—	3.39	7.20	4.12	4.39	5.94	5.77	4.67	5.90
Skewness	—	—	0.38	0.59	-.63	0.16	0.21	-.16	0.11	0.77
<i>Diacodexis secans-kellelyi</i>										
Range	5.00	5.20	3.6-4.5	4.3-5.1	3.8-4.6	4.8-5.6	3.8-4.7	5.6-6.4	3.9-4.3	5.4-6.3
N	1	1	5	6	11	12	34	34	17	16
Mean	5.00	5.20	3.88	4.67	4.25	5.30	4.42	6.03	4.11	5.93
SD	—	—	0.38	0.27	0.25	0.23	0.22	0.21	0.16	0.23
C.V.	—	—	9.80	5.78	5.88	4.34	4.98	3.48	3.89	3.87
Skewness	—	—	0.94	0.32	-.23	-.80	-.56	-.05	-.20	-.56
<i>Diacodexis secans-metsiacus</i>										
Range	3.30	3.30	3.4-4.1	4.4-5.1	3.9-4.4	5.0-5.5	4.1-4.7	4.8-6.3	3.7-4.5	5.1-6.3
N	1	1	6	6	6	6	7	7	6	6
Mean	3.30	3.30	3.82	4.75	4.15	5.20	4.41	5.77	4.12	5.72
SD	—	—	0.26	0.27	0.23	0.19	0.23	0.51	0.31	0.40
C.V.	—	—	6.81	5.68	5.54	3.65	5.22	8.84	7.52	6.99
Skewness	—	—	-.34	0.00	0.00	0.38	-.10	-.85	-.03	-.11



Table 2.—Continued.

Taxa and statistics	P <sup>a</sup>		M <sup>c</sup>		M <sup>d</sup>		M <sup>e</sup>		M <sup>f</sup>	
	L	W	L	W	L	W	L	W	L	W
<i>Diacodexis secans-primus</i>										
Range	5.1-5.6	3.70	3.4-4.0	4.4-5.0	3.7-4.2	4.6-5.4	4.0-4.7	4.9-6.2	3.5-4.6	5.0-6.0
N	2	1	5	5	18	16	15	16	13	13
Mean	5.45	3.70	3.70	4.64	3.94	5.01	4.33	5.68	4.14	5.59
SD	—	—	0.24	0.33	0.15	0.23	0.21	0.30	0.32	0.35
C.V.	—	—	6.49	7.11	3.81	4.59	4.85	5.28	7.73	6.26
Skewness	—	—	0.00	0.69	-0.48	0.23	-0.07	-0.83	-0.29	-0.32
<i>Diacodexis minutus</i>										
Range	4.60	3.10	3.2-3.7	4.5-5.2	3.6-4.0	5.0-5.9	3.6-4.0	5.0-5.9	3.5-4.6	5.0-6.0
N	1	1	5	5	5	5	6	8	13	13
Mean	4.60	3.10	3.52	4.82	3.52	4.82	3.85	5.26	4.14	5.59
SD	—	—	0.20	0.28	0.16	0.28	0.16	0.31	0.32	0.35
C.V.	—	—	5.71	5.81	4.16	5.81	4.16	5.89	7.73	6.26
Skewness	—	—	-0.69	0.32	-0.59	0.32	-0.59	1.20	-0.29	-0.32
<i>Diacodexis gracilis</i>										
UCM 52585	4.80	2.50	3.60	4.00	3.60	4.20	3.90	4.80	3.50	4.40
Artiodactyl sp. A										
Range	—	—	3.6-3.9	4.4-5.0	3.7-4.5	5.4-6.0	3.7-4.5	5.4-6.0	3.4-4.1	5.5-6.3
N	—	—	3	3	4	4	4	4	2	2
Mean	—	—	3.73	4.73	4.13	5.68	4.13	5.68	3.75	5.90
SD	—	—	0.15	0.31	0.33	0.25	0.33	0.25	—	—
C.V.	—	—	4.02	6.55	7.99	4.40	7.99	4.40	—	—

Table 3.—Dimensions of lower teeth of *Diaodexis secans*, lineage segment D. s.-secans.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 22503	CM 34	6.3	2.0			4.6	3.8	4.9	4.4	6.4	4.6
CM 22503	CM 34			6.1	3.3	4.5	3.7				
CM 42125	CM 34	6.2	2.2	5.6	3.0						
CM 55151	CM 34	6.0	2.3								
CM 42097	CM 1084	6.4	2.3								
UCM 42199	CM 34	7.0	2.4	5.8	3.1	4.4	3.4	4.6	4.3	6.7	4.2
CM 55133	CM 34	7.3	2.7								
CM 21213	CM 99			5.2	3.3	4.3	3.9	4.3	4.5		4.7
CM 37300	CM 34			5.6	3.4	4.4	3.6	4.8	4.4	6.4	4.4
CM 55164	CM 34			5.7	2.8						
CM 22532	CM 34			5.3	2.9	4.4	3.6				
CM 40770	CM 34			5.7	2.9	4.7	3.5				
CM 40779	CM 34			5.6	2.5						
CM 22511	CM 90			5.4	2.7	4.3	3.2	4.5	3.9	6.0	4.0
CM 30947	CM 34			5.6	2.9	4.3	3.4	4.6			
CM 21228	CM 34			5.5	3.4	4.6	3.4				
CM 55362	CM 34			5.7	3.0	4.3	3.5				
AMNH 4899*	WRB			5.5	2.7	4.7	3.5	4.8	4.0	6.5	4.0
AMNH 4899*	WRB			5.7	2.8	4.5	3.5	4.8	4.0	6.3	4.0
AMNH 14937**	CM 34			5.7	3.2	4.7	4.1	5.0	5.0		4.8
PU 20598	CM 34			5.3	3.0	4.6	3.7				
PU 20599	CM 34			5.3	2.6	4.5	3.3				
PU 20599	CM 34			4.5	3.6	4.7	4.1	4.7	4.1	6.8	4.5
PU 20800	Aikali Cr			6.2	3.4	4.8	3.8				
CM 43735	CM 1040			5.8	3.0	4.5	4.0				
CM 35732	CM 34					5.0	3.5	5.0	4.1	6.2	4.0
CM 43479	CM 1077					4.8	3.7				
CM 30951	CM 34					4.8	3.7		4.4		
CM 44911	CM 216					4.6	3.7				
UCM 46508	UCM 79041					4.3	3.5				

Table 3.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
		CM 55156	CM 34			4.9		5.2	4.6		
CM 55141	CM 34			4.5	3.5	4.5	4.3			6.8	4.3
CM 55366	CM 34				3.8	5.0	4.5				
CM 30951	CM 34				3.7	4.7	4.5				
CM 55353	CM 34			4.4	3.8						
CM 21020	CM 34			4.9	3.4	4.5	4.4				
CM 21140	CM 34			4.6		4.8	4.3				
CM 22504	CM 34			4.0	3.4	4.4	4.0				
CM 22506	CM 34			4.5	3.9	4.9	4.7				
CM 35777	CM 34			4.5	3.5	4.6	4.5				
CM 55368	CM 34			4.4	3.9	4.4	4.4				
CM 55357	CM 34			4.6	3.8	5.0	4.5				
CM 55167	CM 34			4.4	3.6	5.0	4.5				
CM 42087	CM 1040			4.4	4.0	4.5	4.8				
CM 30944	CM 34			4.5	3.7						
CM 42082	CM 1039			4.4	3.6	4.8	4.5				
CM 42082	CM 1039			4.3	3.5	4.6	4.4				
PU 22317	CM 34			5.1	3.9	5.2	4.5				
PU 22317	CM 34				4.0						
PU 22471	Alkali Cr			4.5	3.3						
CM 35776	CM 34					4.8	4.3				
CM 21017	CM 34					5.3	5.0				
CM 21135	CM 34					4.9	4.4				
CM 21136	CM 34					4.4	4.4				
CM 21137	CM 34					4.7	4.4				
CM 21138	CM 34					5.2	4.6				
CM 22508	CM 34					4.8	4.3				
CM 35771	CM 34					4.7	4.2				
CM 30948	CM 34					4.7	4.4				

Table 3.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 55158	CM 34							4.6	4.4	6.1	4.4
CM 55140	CM 34							4.7	4.3		
CM 40780	CM 34							4.9	4.5		
CM 40764	CM 34							4.8	4.4	6.0	4.2
CM 40764	CM 34									6.3	4.3
CM 40781	CM 34							5.0	4.5		
CM 30945	CM 34								4.2	6.6	4.2
CM 30950	CM 34									5.7	4.8
CM 36441	CM 34							4.8			
CM 37308	CM 34							5.1	4.6		
CM 30946	CM 34							4.4	3.9		
CM 55160	CM 34							4.3	3.9	5.8	4.1
CM 27480	CM 34							5.0	4.6		
CM 30891	CM 34							4.7	4.3		
CM 36931	CM 34							4.6	4.2		
CM 36934	CM 34							4.6	4.3	6.6	4.3
CM 43711	CM 34							5.3	4.3	6.6	4.2
CM 43736	CM 91							5.0	4.5		
CM 44846	CM 1534							5.3	5.3	7.0	4.9
CM 44849	CM 1040							4.5	4.4	6.3	4.3
AMNH 4202***	BHB							4.9	4.8	6.4	4.5
UCM 47026	UCM 81008									6.3	4.5
CM 44909	CM 34									7.1	4.4
CM 43469	CM 34									6.2	4.3
CM 55360	CM 34									6.3	4.5
CM 40784	CM 34									6.8	4.5
CM 36444	CM 34									6.5	4.0
										6.3	4.5



Table 3.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 36445	CM 34										4.6
CM 35772	CM 34									6.6	4.4
CM 35774	CM 34									6.1	4.2
CM 35775	CM 34									6.4	4.1
CM 55359	CM 34										4.1
CM 55168	CM 34										4.0
CM 55169	CM 34									6.1	4.0
CM 42096	CM 34									6.4	4.7
CM 40776	CM 34									5.6	3.7
Mean		6.53	2.32	5.62	3.00	4.53	3.64	4.79	4.41	6.36	4.35
N		6	6	20	20	39	41	53	54	47	52

\* Holotype of *Diacodexis secans*.\*\* Holotype of *Diacodexis olseni*.\*\*\* Holotype of *Diacodexis laticuneus*.

Table 4.—Dimensions of upper teeth of *Diacodexis* secans, lineage segment *D. s.*-secans.

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
CM 21217	CM 99	5.6	4.0								
CM 43476	CM 1040	6.0	3.7	4.1	5.8	4.0	5.9	4.7	6.5	5.0	7.0
CM 55162	CM 34			4.3	5.4						
CM 55351	CM 34			4.0	4.7	4.1	5.3				
CM 35780	CM 34			4.3	4.8	4.5	5.6	4.8	6.0		
CM 22507	CM 34			4.0	5.2	4.6	5.8	5.0	6.6		
CM 42082	CM 1039			4.1	5.1	4.2	5.5	4.8	6.6		
CM 43717	CM 34			4.1	5.0	4.1	5.5	4.6	6.0		6.7
CM 27455	CM 34					4.4	5.3	4.5	5.9		
CM 44908	CM 34					4.6	6.2	5.0	6.9	4.8	6.8
CM 43477	CM 1077							4.8	6.9	4.6	6.5
CM 51636	CM 1096					4.2	6.0				
UCM 44906	CM 34					4.3	5.9				
UCM 46809	UCM 80062					4.4	6.0				
UCM 46811	UCM 80062					4.4	5.9				
CM 42080	CM 1038					4.4	5.5				
CM 21104	CM 34					4.4	5.6				
CM 35782	CM 34					4.5	5.7				
CM 42073	CM 34					4.5	5.5				
CM 42079	CM 1036					4.5	5.6				
CM 40778	CM 34					4.5	5.8			4.5	6.2
CM 37299	CM 34							5.1	6.6		
CM 22532	CM 34							4.7	6.3		
CM 35778	CM 34							5.1	6.8		
CM 37304	CM 34							4.5	6.2		
CM 55166	CM 34							4.5	6.8		
CM 35783	CM 34							5.0	6.6		
CM 55356	CM 34							5.0	7.0		
CM 42074	CM 34							4.8	6.5		



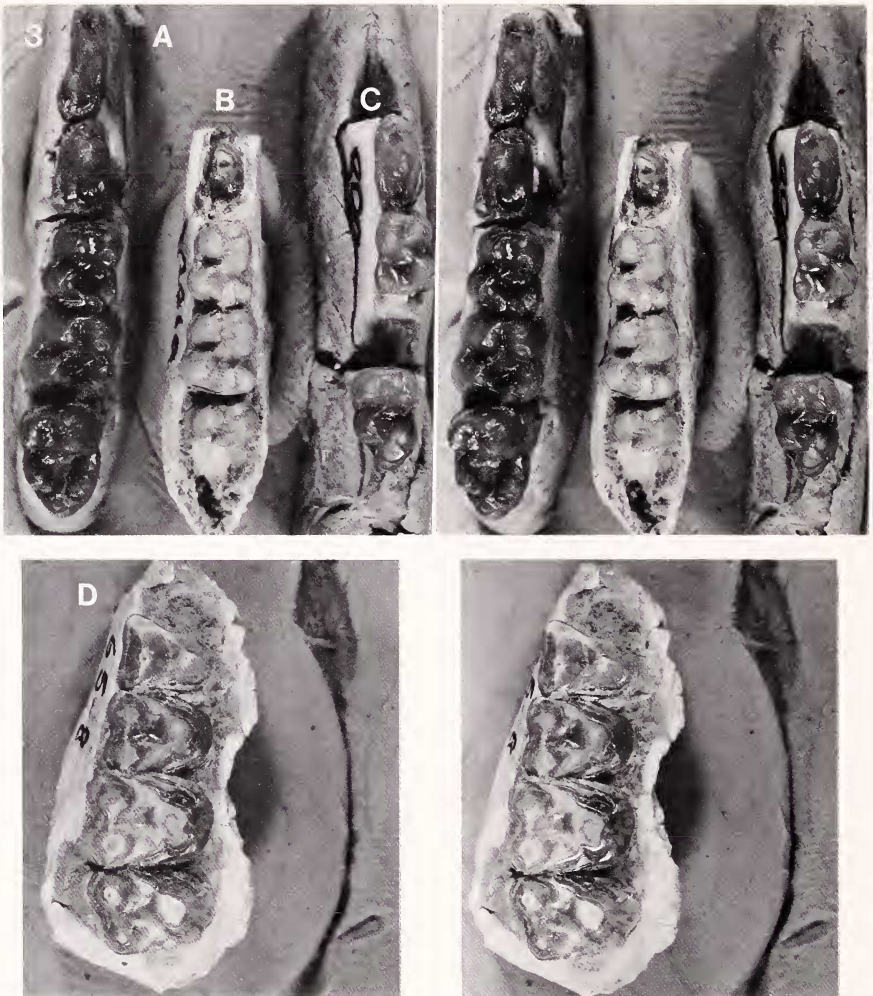


Fig. 3.—*Diacodexis secans* (lineage segment *D. s.-kelleyi*). (A) CM 39880; (B) CM 22810; (C) CM 39221; (D) CM 22803; all approx.  $\times 2$ .

associated upper molars in AMNH 4202 are *Hyopsodus powellianus* (including *H. walcottianus*), a Lysitean-Lostcabinian species.

Lineage Segment *Diacodexis secans-kelleyi*  
(Fig. 3; Tables 1–2, 5–6)

*Etymology*.—In honor of Dana R. Kelley for his contributions to the paleontology of the Lysite Member, Wind River Formation.



*Diagnosis.*—Intermediate in mean size and robusticity of all teeth between lineage segments *D. s.-metsiacus* and *D. s.-secans*. Frequency and degree of expression of the following features higher compared to *D. s.-primus* and *D. s.-metsiacus* and lower compared to *D. s.-secans*: inflation of molar protocones, metaconids, and hypoconids; development of molar postmetacristids and talonid notches; elongation of  $P^3/3$ ,  $P_4$ ; shortness of  $M_3$  talonid. Unlike *D. s.-primus*,  $P^3$  protocone stronger, with metacone (when present) closer to paracone, and lower molars with slightly more medial paraconid.

*Diagnostic series.*—CM 20872, 22801, 22803, 22809–22811, 35932, 37104, 39875, 39880, 39921, 44906; AMNH 4691 (“paratype” of *D. chacensis*); ACM 2405, 2408, 2411, 2674; PU 22540, 22546; UCM 40463.

*Referred specimens.*—CM 19864, 19866, 20872, 20910, 22801–22817, 28688, 28689, 28908, 28924, 28938, 29177, 35930, 35932, 36062, 36063, 36534, 37101–37109, 39218–39220, 39246–39248, 39283, 39469, 39625, 39648, 39649, 39768, 39769, 39871–39880, 39895, 39896, 39906, 39920–39924, 39968, 42095, 42101–42105, 42107–42113, 43708, 43721, 44906, 44912, 53791, 53793, 54124–54126, 54160, 54161, 54212, 54213; AMNH 4691 (“paratype” of *D. chacensis*), 56565; ACM 2403, 2405, 2406, 2408–2414, 2417, 2418, 2512, 2603–2609, 2624, 2671, 2674, 2676, 2680, 2707, 2708, 2738, 2751, 2900, 2901, 2940, 3425, 3475, 3528, 4320, 4324, 4374, 4375, 11070, 11084, 11133, 11134, 11165, 11224, 11251, 11252, 11254; PU 17697, 22540–22542, 22546, 22771, 22772; UCM 40463.

*Localities.*—CM locs. 112, 118, 793, 797, 799, 800, 801, 802, 805, 807, 927, 928, 931, 1007, 1008; ACM locs. 03-425, 03-476, 03-528, 51-L9, 51-L10, 51-L15, 51-L19, 51-L29, 51-L34, 57-28, 57-30, 57-31, 60-112, 60-118, 61-01, 61-02, 62-06, 62-10, 62-11, 62-15, 62-16, 62-17, 62-33, 62-34, 62-35, 62-38, 63-04, 63-06, 63-11, 63-20, 63-28; UCM Loc. 78186 (all Lysitean, Lysite Mbr., Wind River Fm.). CM loc. 1049 (Lysitean or Lostcabinian, Lost Cabin Mbr., Wind River Fm.); AMNH Locs. “*Coryphodon* beds” (Willwood Fm., Bighorn Basin), Huerfano Loc. 8 (Huerfano Fm., Huerfano Basin).

*Known distribution.*—Lysitean to ?Lostcabinian—Wind River Basin (Wind River Fm.), Wyoming; Lysitean—Huerfano Basin (Huerfano Fm.), Colorado. ?Lysitean—Bighorn Basin (Willwood Fm.), Wyoming.

*Discussion.*—*D. s.-kelleyi* overlaps significantly at either end of its range of variation with both the temporally younger *D. s.-secans* and older *D. s.-metsiacus* in size and morphology. Mean values and frequencies of  $P^3/3$  and  $P^4/4$  length, inflation of molar protocones, metaconids and hypoconids, and development of the postmetacristid and talonid notch on  $M_{1-3}$  for *D. s.-kelleyi* are intermediate between those in *D. s.-metsiacus* and *D. s.-secans*. These features, as well as paraconid strength and talonid width on  $M_2$ , show continuous, normally distributed variation in *D. s.-kelleyi*. The protocone on  $P^3$  occurs either di-

Table 5.—Dimensions of lower teeth of *Diagodexis* secans, lineage segment D. s.-kelleyi.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
ACM 2626	ACM 62-11										
CM 22817	CM 807	5.4	1.6		2.4						
CM 39625	CM 802	5.6	1.6								
CM 39768	CM 805			5.3							
CM 39876	CM 797			4.9							
CM 39896	CM 807			4.6							
CM 42107	CM 807			5.3							
CM 54126	CM 807			4.9							
CM 53793	CM 807			4.9							
CM 42105	CM 800			4.8							
CM 42109	CM 797			4.7							
CM 19864	CM 807			5.2		4.2	3.8				
CM 20910	CM 807			4.8		4.3	3.0				
CM 29177	CM 807			5.0		4.5	3.6				
CM 36534	CM 807			5.0		4.2	3.1				
CM 39247	CM 793			5.3		4.3	3.3				
CM 42104	CM 797			4.4		4.5	3.2				
CM 22812	CM 928			4.4		4.5	3.2				
CM 22801	CM 931			4.7		4.2					
ACM 3528	ACM 03-528			4.7		4.3	3.5				
ACM 3528	ACM 03-528			4.9		4.3	3.3				
CM 39906	CM 927			4.7							
PU 22771	CM 797			4.7				4.7	3.7		
CM 39872	CM 797			4.7		4.3	3.6	4.8	4.4		
CM 22805	CM 801			4.5		4.0	3.3	4.4	4.0		
PU 22542	CM 799			4.7		4.2	3.3	4.5	3.8		
PU 22542	CM 799			5.3		4.2	3.4	4.2	4.1		
PU 22542	CM 799					4.0	3.5	4.3	4.0		
AMNH 4691*	CM 799			5.1		4.1	3.1	4.4	3.6		3.6
	Coryphodon beds			4.7		4.6	3.5	4.8	4.1		4.0

Table 5.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 42103		4.2	2.5	4.1	3.3	4.4	3.7				
CM 43708		4.6	2.1					5.4		3.4	
CM 39921		4.7	2.5					5.0		3.3	
CM 39921		4.5	2.4	4.2	3.4						
CM 39880		4.9	2.9	4.3	3.6	4.5	4.4			6.0	3.1
CM 22809		4.8	2.6					3.8		5.8	3.7
ACM 2403		5.2	2.5	4.1	3.1	4.2	3.9				
CM 22810		4.2	2.3	4.0	3.0	4.2	3.7				3.5
CM 22810				4.3	3.1	4.2	3.8			6.0	4.1
CM 20872			2.6	4.3	3.4	4.4	3.8			6.0	4.1
CM 37104				4.6	3.6	4.8	4.3			6.0	3.6
AMNH 56565	Huercifano 8			4.5	3.0						
CM 44906				4.1	2.8						
CM 54212				4.1	3.2						
CM 799											
CM 54213				4.1	3.2	4.7	3.6				3.5
CM 22811				4.3	3.0	4.3					
CM 42112				4.5	3.5	4.5	4.0				
CM 42108				4.5	3.4	4.7	4.2				
CM 54125				4.0	3.2	4.6	3.7				
CM 42095				4.2	3.2						
CM 37106				4.1	3.5	4.5	3.6			5.4	3.4
CM 28924				4.2	3.4	4.5	4.3				
CM 19866				4.1	3.2	4.2					
CM 37106				4.1	3.2	4.5	3.6			5.6	
CM 39873				4.1	3.2	4.3	3.8			5.7	3.5
CM 39920				4.3	3.0	4.5	4.0				
CM 22802				4.0	4.0	4.0	3.8				
CM 39871				4.2	3.3	4.4	4.4				
CM 36062				4.3	3.3	4.6	4.0			6.0	3.7

Table 5.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 22807	CM 799					4.5	3.6				
CM 42102	CM 800					4.4	3.6				
PU 22772	CM 799					4.2	3.2				
ACM 2512	ACM 62-35					4.4	3.4	4.4	3.9		
ACM 2900	ACM 61-01					4.2	3.5				
ACM 2410	ACM 62-16					4.2	3.6				
ACM 2680	ACM 61-01					4.2		4.7	4.2		
ACM 4324	ACM 63-11							4.3	4.0		
ACM 2607	ACM 57-30							4.3	3.5		
ACM 2624	ACM 57-31							4.5	4.1		
CM 39879	CM 929							4.9	3.8		
CM 39218	CM 931							4.7	4.0		
CM 39922	CM 800							4.6			
CM 28908	CM 797							4.6	4.2		
CM 37105	CM 931							4.9	4.5		
CM 39469	CM 112							4.8	4.1		
CM 22814	CM 807							4.5	3.9		3.7
CM 22814	CM 807							4.5	4.2		
CM 39283	CM 112							4.8	4.3		
CM 42113	CM 797							4.7	4.0		
CM 37101	CM 807							4.0	4.2		
CM 37102	CM 807							4.3	4.1		
CM 39874	CM 797							4.5	4.0		
CM 39875	CM 797							4.8	4.5		
CM 39968	CM 928							4.3	4.0		
CM 22806	CM 799							4.5	3.5		
UCM 40463	CM 797							3.7			3.5
PU 17697	CM 799							4.7	4.2		4.0
ACM 11251	ACM 51-L34							4.2	3.5		3.4
ACM 11252	ACM 51-L34							4.2	4.2		4.0



Table 5.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
ACM 3425	ACM 03-425							4.7	4.1		3.5
ACM 2405	ACM 62-06							4.2	4.2	5.6	3.4
ACM 2708	ACM 60-118							4.2	4.0	5.1	3.6
ACM 2408	ACM 62-15							4.2	3.7	5.6	3.7
ACM 2751	ACM 60-118							4.2	4.1		
CM 22813	CM 799									5.7	4.0
CM 22816	CM 807									5.6	3.5
CM 36063	CM 799									6.0	4.0
CM 37103	CM 807									5.5	3.4
CM 37108	CM 797									5.6	3.9
CM 37109	CM 807									5.6	3.6
CM 39769	CM 805									6.0	4.0
CM 39877	CM 797									6.0	3.8
CM 39923	CM 800									6.1	3.7
CM 42101	CM 799									6.1	3.9
PU 22541	CM 799									5.6	3.4
ACM 2608	ACM 57-28									5.2	3.7
ACM 2409	ACM 62-33									5.3	3.7
ACM 2406	ACM 62-34									5.5	3.8
ACM 11133	ACM 51-L15									6.3	4.0
ACM 11134	ACM 51-L15									5.5	3.5
ACM 11165	ACM 51-L19									5.7	3.8
ACM 11254	ACM 51-L34									6.2	3.8
ACM 3475	ACM 03-476									5.5	3.7
ACM 4375	ACM 63-04									5.9	3.8
ACM 4375	ACM 63-04									6.4	3.8
CM 44912	CM 1007									5.6	3.6
Mean		4.80	2.61	4.25	3.31	4.47	3.97	5.73	3.72		
N		34	36	49	47	58	56	50	52		

\* "Paratype" of *Diacodexis chalcensis* (Cope, 1884).

rectly lingual to the paracone (CM 35932) as in *D. s.-metsiacus* and *D. s.-primus* or slightly more posteriorly (ACM 2674), but not as posteriorly as in *D. s.-secans*. Presence of a P<sup>3</sup> metacone is variable. Both the postmetacristid and talonid notch on M<sub>1-3</sub> occur more frequently than in *D. s.-metsiacus*, but are weakly developed, even on the robust specimens that overlap in size and degree of cusp inflation with *D. s.-secans*. Compared to the latter, the protocone on M<sup>1-3</sup> of *D. s.-kelleyi* is less bulbous, resulting in a more distinct postprotocrista, pseudo-hypocone, cingular hypocone, and pericone, and more complete isolation of the metaconule from the postprotocrista. The cingular hypocone and pericone are better and more frequently developed than in *D. s.-primus* and *D. s.-metsiacus*. On ACM 2417, the extreme development of the pericone distends the anterolingual base of the crown. Some of the upper molars, especially M<sup>3</sup>, have an incipient mesostyle at the base of the centrocrista, as well as slight swelling on the ectoingulum labial to the centrocrista.

CM 39921, 54212 and 44906 are the smallest and most gracile in the *D. s.-kelleyi* sample, whereas CM 39880, 39874, 39875, and 28924 are the largest and most robust. These specimens show the greatest degree of overlap with *D. s.-metsiacus* and *D. s.-secans*, respectively. Isolated P<sub>4</sub>s and M<sub>1</sub>s of *D. s.-kelleyi* exhibit to a much lesser degree the morphological differences (cusp inflation, larger size) between this lineage segment and *D. s.-metsiacus* than do M<sub>2</sub>s and M<sub>3</sub>s.

On CM 37104 the cristid obliqua on M<sub>1</sub> extends weakly to the metaconid in a manner somewhat reminiscent of *Antiacodon*; this feature occurs much more frequently on M<sub>1</sub>s of *D. s.-metsiacus*. However, the molars on CM 37104 as well as those of both lineage segments differ from those of *Antiacodon* in being more bulbous (inflated hypoconid, metaconid, and paraconid), and in having a much shallower talonid and trigonid basin, a smaller hypoconulid, a weaker cristid obliqua that is not directed toward the metaconid on M<sub>2-3</sub>, and a lower, less compressed trigonid. Similarly, CM 22810 resembles *Hexacodus uintensis* in size and position of the molar cusps, but lacks many of the derived features of the latter—the strong hypocristid directed toward the entoconid, the broad postcingulid, the high and conical entoconid, the severely reduced paraconid, and the elevated paraconid and metaconid.

The three small specimens of *D. s.-kelleyi* listed above also approach *D. minutus* in size and morphology except for the slight metaconid inflation on M<sub>1</sub> and the weaker postmetacristid and talonid notch on M<sub>1</sub> and M<sub>3</sub>. These specimens may well represent the most primitive expression of *D. minutus*, but referral to the latter is unwarranted at this point, given that they preserve only P<sub>4</sub>, M<sub>1</sub>, and M<sub>3</sub>, which are less diagnostic than M<sub>2</sub>. The M<sub>3</sub> in CM 39921 is indistinguishable from

$M_3$ s of Gardnerbuttean *D. minutus*, yet this and other small specimens fall within the lower part of the range of variation of *D. s.-kelleyi*. Importantly, the entire range of morphological variation (normally distributed) of *D. s.-kelleyi* includes the incipient and/or moderate development of features ( $P^3/3$  elongation; molar postmetacristid, talonid notch, metaconid inflation, paraconid reduction; squareness of  $M_{1-2}$ ) that appear to be canalized and amplified (in frequency and degree of expression) in temporally younger *D. s.-secans*, *D. woltonensis*, and *D. minutus*.

Lineage Segment *Diacodexis secans-metsiacus*  
(Fig. 4; Tables 1–2, 7–8)

*Diagnosis.*—Smaller (mean size) and less robust than lineage segment *D. s.-kelleyi* and *D. s.-secans*, with  $P_2$  and  $P^3/3$  shorter,  $P^3$  protocone smaller,  $P_3$  shorter than  $M_3$ , molars less bunodont,  $M_{1-2}$  less nearly square, less inflated molar protocones, conules, protoconids, metaconids, hypoconids and more distinct protocristae, conulecristae and pseudohypocones;  $M_{1-3}$  postmetacristid often absent or extremely weak, talonid notch weak; slightly smaller (mean size) than lineage segment *D. s.-primus* with  $P_3$  usually longer,  $P_4$  postmetacristid present,  $P_4$  paraconid usually double, molar paraconids slightly medial relative to metaconid, talonid notch present, shorter  $M_3$  hypoconulid lobe,  $P^3$  metacone stronger and closer to the paracone.

*Diagnostic series.*—CM 12419; AMNH 4696 (cotype of *D. metsiacus*), 4700 (holotype of *D. brachystomus*), 15522, 15666; UCM 19427, 52551–52553; USGS 2352.

*Referred specimens.*—CM 12368, 12395, 12396, 12419, 53912, 58131, 58132, 58134, 58137; AMNH 4696 (cotype of *D. metsiacus*), 4700 (holotype of *D. brachystomus*), 15522, 15666; UCM 19427, 44125–44128, 44131, 45778, 45783, 47604, 52551–52578, 52586–52598; USGS 2352.

*Localities.*—CM locs. 147, 673, 843; UCM locs. 80024, 80066, 81092, 84168, 84172, 84177, 84178, 84180, 84181, 84183, 84248, 84249, 84254, 84255, 85227, 85237, 85257, 85258; AMNH locs. *Coryphodon* beds, St. Joe, Dorsey Creek; (all late Graybullian, Willwood Fm.), Bighorn Basin, Wyoming.

*Known distribution.*—Early Wasatchian (late Graybullian)—Bighorn Basin (Willwood Fm.), Wyoming.

*Discussion.*—The material referred to the lineage segment *D. s.-metsiacus* includes the holotype of *D. brachystomus* and the cotype of *D. metsiacus*. These specimens are at the opposite ends of the range of variation of normally distributed and penecontemporaneous samples from the *Bunophorus* interval zone of the Willwood Formation (late Graybullian). Features that distinguish these two specimens are con-

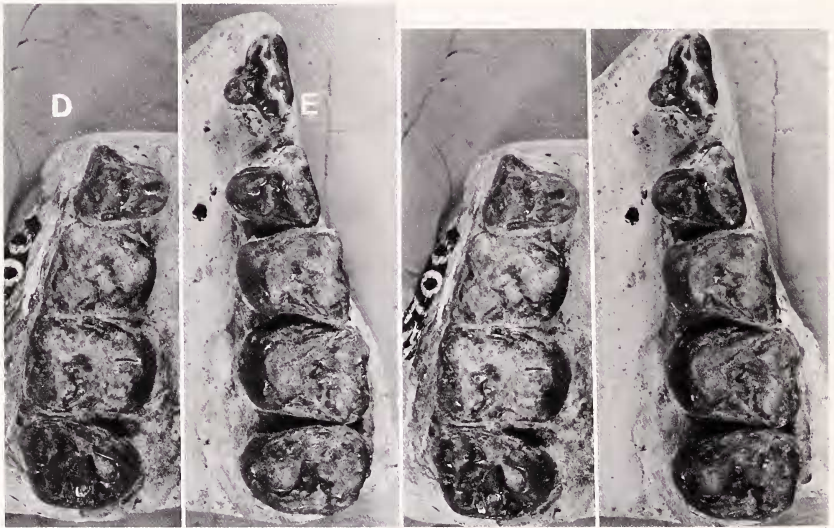
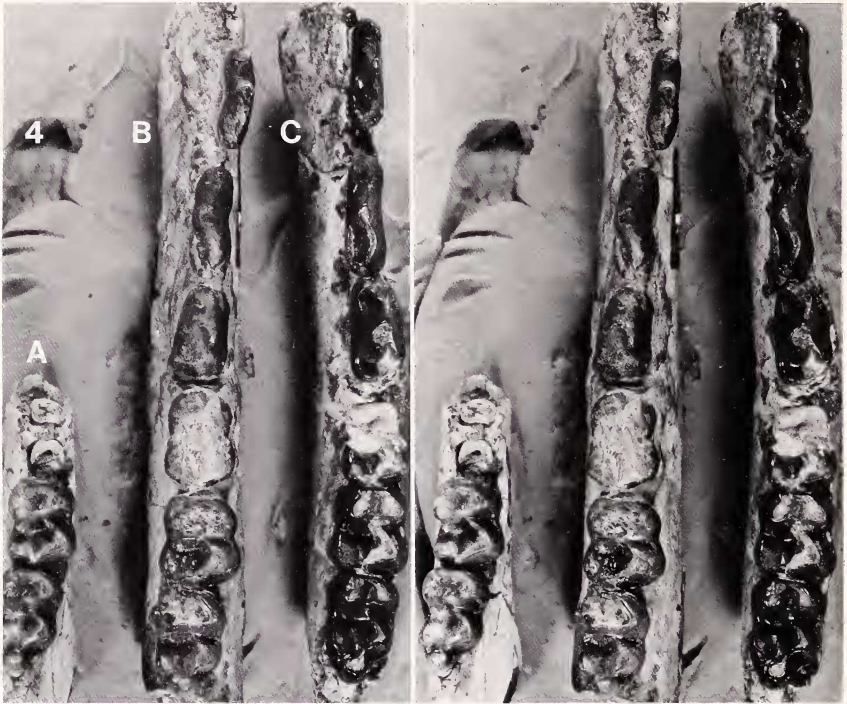
Table 6.—*Dimensions of upper teeth of Diacodexis secans, lineage segment D. s.-kelleyi.*

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
ACM 2674	ACM 60-115	5.0	5.2								
CM 43721	CM 797		4.5	3.6	4.3						
ACM 2411	ACM 62-36					3.8	4.8	3.8	5.6	3.9	5.4
CM 22802	CM 799		5.1	4.5	5.1	4.5	5.5	4.4	6.2	4.2	6.0
CM 22803	CM 799		4.6	4.1	4.6	4.1	5.2	4.4	6.0	4.1	6.0
CM 22808	CM 807		4.7	4.6	4.7	4.6	5.5	4.4	5.9	4.2	5.8
CM 35932	CM 929		4.8	3.7	4.8	4.4	5.6	4.4	6.4	4.2	6.0
CM 28688	CM 807			4.0	4.5	4.0	5.3	4.5	6.3	4.2	6.0
CM 54124	CM 807			4.2	5.3	4.2	5.3	4.3	5.9	4.0	6.0
PU 22540	CM 799			4.4	5.4	4.4	5.4	4.7	6.0		
CM 53791	CM 807				5.3						
ACM 2603	ACM 57-30			4.0	5.0	4.0	5.0				
ACM 2606	ACM 57-30			4.2	5.2	4.2	5.2				
ACM 4375	ACM 63-04			4.5	5.5	4.5	5.5				
ACM 2417	ACM 62-38										
CM 39246	CM 793							4.1	6.0	3.9	5.6
CM 22815	CM 807							4.1	5.6	3.9	5.9
CM 39649	CM 802							4.4	6.0	4.3	5.7
CM 42111	CM 797							4.3	6.1	3.9	
CM 35930	CM 929							4.3	6.2	4.3	
CM 28938	CM 797							4.4	6.2	4.4	
CM 39648	CM 802							4.5	6.3	4.5	
CM 39248	CM 793							4.3	6.0	4.3	
CM 37107	CM 931							4.5	6.0	4.5	
CM 39219	CM 931							4.2	6.0	4.2	



Table 6.—Continued.

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
CM 54160	CM 807							4.7			
CM 39220	CM 931							4.6	6.0		
CM 54161	CM 807							4.5	6.0		
CM 39924	CM 800							4.4	5.9		
CM 39924	CM 800							4.3	5.8		
CM 39906	CM 927							4.5	6.0		
CM 39906	CM 927							4.5	6.2		
ACM 2604	ACM 57-30							4.4	6.0		
ACM 2605	ACM 57-31							4.5	5.9		
ACM 2609	ACM 57-31							4.6	5.8		
ACM 2412	ACM 62-17							4.4	6.0		
ACM 2413	ACM 62-10							4.0	5.7		
ACM 2414	ACM 62-11							4.7	6.3		
ACM 2901	ACM 61-02							4.7	6.3		
ACM 2940	ACM 61-02							4.5	5.8		
ACM 11084	ACM 51-L10							4.5	6.3		
ACM 2418	ACM 62-38									4.3	6.0
ACM 4375	ACM 63-04									4.3	6.2
ACM 11070	ACM 51-L9									4.0	5.9
CM 28689	CM 807									4.2	6.2
CM 28689	CM 807									4.2	6.3
CM 42110	CM 797									4.0	5.8
CM 39878	CM 797									4.3	6.0
Mean		3.88	4.67	4.25	5.30	4.41	6.03	4.41		4.11	5.93
N		5	6	11	12	34	34	17		16	16



tinuously variable among these samples and include size, trigonid elevation, and degree of molar (especially metaconid) inflation.

The holotype of *D. brachystomus* and the other larger specimens in *D. s.-metsiacus* overlap morphologically with material in the lower part of the range of variation of *D. s.-kelleyi* and with *D. s.-primus* in size, whereas the cotype of *D. metsiacus* is remarkably similar to some of the late Graybullian and/or early Lysitean material from the San Juan and Piceance basins assigned to *Artiodactyla* sp. A (see below). Resemblances here include small size and an elevated paraconid-metaconid wall on  $M_{1-3}$ , one of the major derived features of *Artiodactyla* sp. A. The latter is further derived in having higher trigonids, broad postcingulids, and strong, isolated hypoconulids close to tall entoconids on the molars. As in *D. s.-metsiacus*, the molar metaconids on the cotype of *D. metsiacus* are slightly more inflated than in *Artiodactyla* sp. A and the postcingulids and hypoconulids are weak. As such, the range of variation in *D. s.-metsiacus* includes some of the derived features that are increased in the frequency and degree of expression in *Artiodactyla* sp. A on the one hand and *D. s.-kelleyi* on the other.

Rose (1982) concluded that the skeleton of *Diacodexis* was too specialized for the genus to be ancestral to the Suina and some extinct non-ruminants. However, his observations apply only to two specimens of *D. s.-metsiacus* rather than *Diacodexis* as a whole; skeletal features of *D. s.-metsiacus* may have varied as much as do the dental ones (R. Bakker, personal communication concerning the distal fusion of the tibia and fibula). Also, if skeletal evolution in *Diacodexis* tracked our reconstruction of dental evolution, the skeleton of *D. s.-primus* (unknown) may have been less specialized in some features; in any event, there is no *a priori* reason to assume that its skeleton was as specialized as the two specimens of *D. s.-metsiacus*. If elongate limbs and a fused distal tibia and fibula characterize *D. s.-metsiacus* (Rose, 1982), they should also occur in subsequent lineage segments of *D. secans*, as well as *D. minutus*, *D. woltonensis*, antiacodontids, homacodontids, and leptchoerids, following our reconstruction of the evolutionary relationships of these taxa based on dental evidence. These features are known in *Antiacodon pygmaeus*, *Homacodon vagans* (West, 1984), *Leptochoerus* (Marsh, 1894; Edwards, 1976), and *D. minutus* (see below).

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Fig. 4.—*Diacodexis secans* (lineage segment *D. s.-metsiacus*). (A) AMNH 4696 (cotype of *D. metsiacus*); (B), (D) and (E) AMNH 4700 (holotype of *D. brachystomus*); (C) AMNH 15666; all approx.  $\times 2$ . Note that the left  $P^3$  in (E) is permanently mounted in the right maxilla.

Table 7.—Dimensions of lower teeth of *Diacodexis secans*, lineage segment D. s.-metsiacus.

Specimen no.	Locality	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W	L	W
AMNH 4700*	Willwood	5.0	1.5	5.6	2.0	4.7	2.8	3.5	4.0	4.5	4.0	5.4	3.4
AMNH 4700	Fm.		1.6	5.5		4.5	2.6	4.2	3.4	4.3	3.9	5.5	3.6
AMNH 15666**	Dorsey			5.8	2.2	5.0	2.8		3.4	4.3	4.0	5.4	3.7
AMNH 15666	Creek	5.4	1.9	5.8	2.2	5.1	2.9	3.5	4.0	4.3	4.0	5.4	3.7
AMNH 15522	2 mi E	5.5	2.0			5.0	2.7	4.1	3.3	4.3	3.7	5.4	3.4
AMNH 15522	St. Joe					5.0	2.7	4.2	3.2	4.2	3.7	5.1	3.3
UCM 52565	UCM 84248			5.0	2.0	4.4	3.4	4.1	3.1				
UCM 52565	UCM 84248							4.1	3.1	4.3	3.3		
UCM 52551A	UCM 84183					4.8	2.8	4.1	3.1				
UCM 52551B	UCM 84183					4.6	2.7	4.1	3.0		3.5		
UCM 52551C	UCM 84183					4.8	2.6	4.1	3.3				
UCM 52556A	UCM 85258					5.0	2.6			4.7	3.9		
UCM 52556B	UCM 85258					4.9		4.1	3.1	4.6	3.7		
UCM 52558	UCM 84183					4.9	2.8	4.4	3.4	4.6	3.8		
UCM 52560	UCM 84177					5.7	3.1	4.5	4.1	4.5	4.1		
UCM 52562A	UCM 84178					4.7	3.0	4.1	3.2	4.4	4.0		
UCM 52562B	UCM 84178					4.7	2.5	4.2	3.3	4.5	3.7		
UCM 52563	UCM 84254					4.7	2.4	4.1	3.0	4.5	3.4		
UCM 52566	UCM 84168					4.8	2.2					5.2	3.4
UCM 52570	UCM 84178					5.2	2.9	4.2	3.4	4.6	4.0		
UCM 52571	UCM 84249					4.9	3.6	4.5	3.6			5.2	3.6
UCM 52571	UCM 84249					5.0	3.6						
UCM 52572	UCM 84254					5.2	3.0	4.2	3.3	4.4	3.6		
UCM 52573	UCM 84227					5.4	2.5			4.3	3.6	4.8	3.4
UCM 52574	UCM 84178					5.0	2.9	4.1	3.2	4.2	3.8		
UCM 47604	UCM 81092					5.3	2.9	4.1	3.2	4.3	3.8		
UCM 45778	UCM 82022					4.9	2.5	4.2	3.1	4.5	3.7		
CM 58131	CM 843						2.6	3.9	3.4	4.1	4.0	5.4	3.6
CM 58132	CM 843						2.7	4.1	3.2	4.3	3.7		3.3
CM 53912	CM 843						2.6	4.4	3.5				
CM 12419	CM 673						2.5	4.3	3.4	4.6	4.2		4.2
CM 12368	CM 147					5.1		4.2	3.6	4.5	4.2		3.8
UCM 52568	UCM 85259							4.3	3.2	4.6	4.5	5.8	3.8
UCM 52578	UCM 84178							4.3	3.2	4.6	4.6	4.8	3.5
UCM 45783	UCM 80024								3.4	4.6	4.1		3.7
UCM 44123	UCM 80066							4.5	3.2	4.2	4.2		3.6
										4.7	4.7		3.9

Table 7.—Continued.

Specimen no.	Locality	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W	L	W
UCM 44126	UCM 80066					4.2	3.3	4.4	3.6				
UCM 52551E	UCM 84183			4.2	3.5	4.4	3.5	4.4	3.6			5.4	3.5
UCM 52551F	UCM 84183			4.1	3.2	4.3	3.2	4.3	3.8			5.0	3.5
UCM 52551H	UCM 84183			3.9	3.0								
UCM 52552	UCM 84181			3.7	3.0			4.5	3.6				3.4
UCM 52557	UCM 85260			4.1	3.3	4.2	3.3	4.2	3.6			4.7	3.2
UCM 52555	UCM 84178				3.0	4.2	3.5	4.2	3.5			5.0	3.3
UCM 52551D	UCM 84183					4.5	3.8	4.5	3.8				
UCM 52551G	UCM 84183					4.0	3.8	4.0	3.8			4.6	3.4
UCM 52554	UCM 84249					4.3	3.5	4.3	3.5			5.1	3.2
UCM 52559	UCM 85227					4.3	3.6	4.3	3.6			5.4	3.1
UCM 52561	UCM 84178					4.3	4.0	4.3	4.0			5.1	3.5
UCM 52564	UCM 84172					4.0	3.2	4.0	3.2			5.1	3.2
CM 58137	CM 843					4.0	3.6	4.0	3.6				
CM 58134	CM 843					4.3	3.5	4.3	3.5			3.4	
CM 12395	CM 843					4.2	3.5	4.2	3.5			5.2	3.3
CM 12396	CM 843					4.6	4.0	4.6	4.0			5.5	3.5
UCM 52567	UCM 84183					4.5	3.7	4.5	3.7			5.3	3.4
UCM 52569	UCM 85257					4.6	3.9	4.6	3.9			5.1	3.5
UCM 52575	UCM 85237					3.6	3.6	3.6	3.6			5.6	3.5
UCM 44128	UCM 80066					4.3	3.3	4.3	3.3			5.0	2.9
CM 19427	CM 843					4.1	3.7	4.1	3.7			5.0	3.3
UCM 44127	UCM 80066					4.0	3.4	4.0	3.4			4.7	4.0
AMNH 4696***	Coryphodon beds					4.1	3.3	4.1	3.3			5.0	3.2
UCM 52551I	UCM 84183											5.1	3.3
UCM 52551J	UCM 84183											5.4	3.7
UCM 52551K	UCM 84183											5.0	3.4
UCM 52551L	UCM 84183											5.0	3.2
Mean		5.30	1.75	5.54	2.10	4.95	2.79	4.16	3.27	4.36	3.73	5.17	3.43
N		3	4	5	4	28	29	32	39	50	52	34	38

\* Holotype of *Diacodexis brachystomus*.\*\* Pleistotype of *Diacodexis chiacensis*.\*\*\* Cotype of *Diacodexis metisiacus*.



Table 8.—Dimensions of upper teeth of *Diacodexis secans*, lineage segment *D. s.-metsiacus*.

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
AMNH 4700*	Willwood		3.3	3.8	4.5	4.4	5.5	4.7	6.3	4.5	6.3
AMNH 4700	Fm.			4.1	4.4	4.4	5.0	4.6	6.3	4.2	5.9
AMNH 15666**	Dorsey Cr			4.1	5.1	4.2	5.2				
UCM 52577	UCM 84255			3.4	4.7	3.9	5.0	4.1	5.6	4.0	5.6
UCM 52567	UCM 84183			3.7	5.0	3.9	5.3	4.3	4.8	3.7	5.1
UCM 52553	UCM 84248			3.8	4.8	4.1	5.2	4.4	5.9	4.4	5.8
UCM 52576	UCM 84180							4.6	5.8	4.4	5.8
UCM 52566	UCM 84168							4.2	5.7	3.9	5.6
Mean				3.82	4.75	4.15	5.20	4.41	5.77	4.12	5.72
N				6	6	6	6	7	7	6	6

\* Holotype of *Diacodexis brachystomus*.\*\* Pleistotype of *Diacodexis chacensis*.

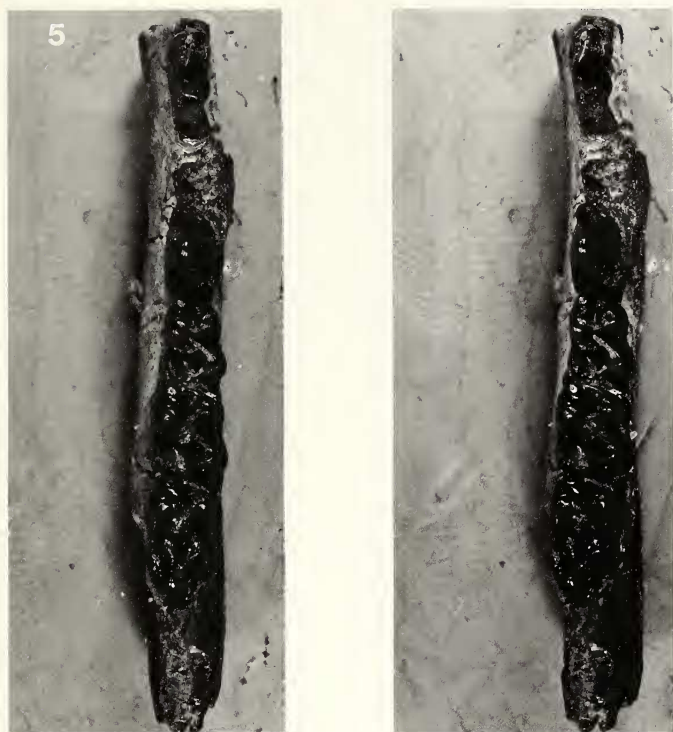


Fig. 5.—*Diacodexis secans* (lineage segment *D. s.-primus*). AMNH 15672; approx.  $\times 2$ .

Lineage Segment *Diacodexis secans-primus*  
(Fig. 5; Tables 1–2, 9–10)

*Etymology.*—*primus*, L., first, earliest; in allusion to the earliest known occurrence of *D. secans*.

*Diagnosis.*—Differs from the other lineage segments of *D. secans* as follows: complete lack of a  $P_4$  postmetacristid, a talonid notch and a postmetacristid on the molars;  $P_{3-4}$  shorter;  $M_{1-3}$  talonid basin closed lingually by a pre-entocristid;  $M_3$  usually longer with an elongate hypoconulid lobe; more frequent occurrence of a partial or complete hypoconid-entoconid connection on  $M_3$ ; molar paraconids directly anterior to metaconids; compared to *D. s.-kelleyi* and *D. s.-secans*,  $P^3$  protocone weaker, with metacone (when present) closer to metastyle;  $P_3$  shorter than  $M_3$ , molar protocones less inflated with more distinct protocristae, conulecristae, conules and pseudohypocones.

*Diagnostic series.*—CM 12258, 36810; AMNH 15527, 15671, 15672; UCM 19388, 38121, 49404; UW 7544, 7571, 9213.

Table 9. — *Dimensions of lower teeth of Diacodexis secans, lineage segment D. s.-primus.*

Specimen no.	Locality	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W	L	W
CM 36805	CM 878	3.0	1.5										
AMNH 15672	Shoshone R.	4.0	1.6			4.4	2.7	4.0	3.2	4.6	3.9	6.0	3.9
AMNH 15527*	Elk Cr			4.8	1.7	4.6	2.4	4.0	3.0	4.4	3.7	6.0	3.6
	CM 17472			4.9	2.0	5.0	2.8	4.2	3.4				
	UW 7571			4.7	1.9	4.7	2.5	4.1	3.3	4.3	4.0	6.2	4.0
	UW 7544					4.4	2.3	4.2	2.9	4.7	3.7	6.0	3.8
	CM 57693				1.7	4.8	2.5	4.0	3.2				
UCM 49403	UCM 81003			5.0	1.9								
UCM 52579	UCM 84195					4.5	2.9	4.2	3.3	4.3	4.2	5.0	3.5
CM 12244	CM 140					4.8	2.4						
CM 12291	CM 678					4.6	2.4		3.1				
CM 34338	CM 141					4.9	2.4						
CM 34363	CM 187					4.7	2.5						
CM 36653	CM 878								3.3	4.7	3.9		
CM 57694	CM 878					4.8	2.7						
UCM 19388	Elk Cr					4.5	2.2	4.0	2.9	4.5	4.2	6.0	4.0
UCM 49410	UCM 81003					5.0	2.4						
CM 39361	CM 953					4.2	2.2						
CM 39361	CM 953					4.4	2.4						
CM 39360	CM 953					4.3	2.2						
CM 39360	CM 953					4.3	2.1						
CM 12188	CM 150									3.3	4.2	6.0	3.8
CM 34310	CM 142							4.1		4.7	3.9		
CM 36186	CM 878								3.4	4.6	4.0		
UCM 19468	CM 187								3.0	4.3	3.9	5.9	3.6
UCM 20934	CM 187							3.9	3.3	4.6	4.0		
UCM 49408	UCM 81003							4.2	3.4				
UCM 49406	UCM 81003							4.0	3.0				
UCM 49407	UCM 81003							4.2	3.2				
UCM 49402	UCM 81003							4.3	3.3				

Table 9. —Continued.

Specimen no.	Locality	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W	L	W
UCM 49401	UCM 81003							4.2	3.3				
CM 38873	CM 953							4.1	3.2	4.3	3.8		
CM 38872	CM 953							3.8	3.0				
CM 38874	CM 953							4.0	3.1				
CM 38871	CM 953							4.0	2.9				
CM 34351	CM 678							3.9		4.5	3.8		
CM 36181	CM 878								3.1	4.4	3.6		
UCM 52581	UCM 84195							4.5		4.5	4.1		
CM 36817	CM 878							5.0	4.1	5.0	4.1	5.8	4.0
CM 12207	CM 154							4.4	4.0	4.4	4.0	6.0	4.0
CM 12167	CM 149							4.6	3.8	4.6	3.8	6.1	3.9
CM 12227	CM 187							4.3	3.9	4.3	3.9	5.5	3.5
CM 12260	CM 140							4.4	3.8	4.4	3.8	6.0	3.5
CM 12259	CM 140							4.7	3.9	4.7	3.9	6.1	3.8
CM 12258	CM 140							4.4	3.8	4.4	3.8	5.4	3.5
CM 17470	CM 681							4.6	3.9	4.6	3.9	6.3	4.0
CM 36207	CM 878											3.5	3.5
CM 36213	CM 878											3.9	3.7
CM 36650	CM 878									4.7	3.9		
CM 36708	CM 878							5.0	4.1	5.0	4.1		
CM 36807	CM 878							4.4	3.8	4.4	3.8		
CM 36810	CM 878							4.7	3.8	4.7	3.8	5.8	3.6
CM 36811	CM 878							4.5	4.0	4.5	4.0		
CM 36812	CM 878							4.3	3.6	4.3	3.6		
CM 58136	CM 1093											4.1	4.0
CM 58135	CM 1093											4.3	3.8
UCM 19393	CM 677									4.3	4.0	5.6	4.0
UCM 49404	UCM 81003							4.0	4.2	4.0	4.2		
UCM 49400	UCM 81003							4.9	4.1	4.9	4.1		
								4.5	3.9	4.5	3.9		

Table 9.—Continued.

Specimen no.	Locality	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W	L	W
UCM 49397	UCM 81002									4.5			
UCM 49413	UCM 83198									4.5			3.7
UCM 49414	UCM 83198									4.9			3.7
CM 38874	CM 953									4.2			3.6
CM 38874	CM 953									4.4			3.8
CM 12231	CM 153									4.7			4.1
UCM 52580	UCM 84198											6.7	4.2
UCM 52580	UCM 84198											5.7	3.9
CM 28957	CM 157											5.9	3.7
CM 34325	CM 678											5.6	3.6
CM 36183	CM 878											6.2	3.9
CM 36185	CM 878											5.4	3.6
CM 36182	CM 878											5.7	3.8
CM 36209	CM 878											5.2	3.5
CM 36212	CM 878											5.6	3.8
CM 36651	CM 878											5.9	3.7
CM 37434	CM 878											6.3	3.7
CM 37433	CM 878											5.6	4.1
CM 37436	CM 878											6.7	
CM 38127	CM 878												3.4
CM 36604	CM 878												3.7
UCM 40352	CM 187											5.5	3.5
UCM 49399	UCM 81003											5.5	3.5
UCM 49136	UCM 81002											5.8	3.7
CM 38876	CM 953											5.5	3.5
Mean		4.85	1.84	4.61	2.46	4.07	3.17	4.51	3.89			5.83	3.75
N		4	5	18	19	20	25	40	41			39	39

\* "Plesiotype" of *Diacodexis chacensis*.



*Referred specimens.*—In addition to material referred elsewhere (McKenna, 1960; Delson, 1971; Bown, 1979), CM 12167, 12188, 12207, 12227, 12231, 12244, 12258–12260, 12291, 12301, 17467, 17470, 17472, 28956, 28957, 28974, 34310, 34325, 34338, 34351, 34363, 36175, 36177, 36179, 36181–36183, 36185, 36186, 36204, 36207–36213, 36602–36604, 36650, 36651, 36653, 36708, 36801–36805, 36807–36814, 36816, 36817, 36870, 37433–37436, 37438, 37439, 38126–38129, 38865–38876, 39360, 39361, 53709, 53724, 57693, 57694, 58135, 58136; AMNH 15527, 15671, 15672; UCM 19388, 19393, 19468, 20934, 38121, 40352, 49136, 49137, 49397, 49399–49411, 49413, 49414, 52579–52581; UW 7544, 7571, 7577, 9215, 9996.

*Localities.*—CM loc. 953 (Sandcouleean, Wasatch Fm.), Colorado. UCM locs. 81003, 81002, 83198 (Sandcouleean—early Graybullian, “Wasatch Fm.”), Wyoming. CM locs. 140, 141, 142, 149, 150, 153, 154, 157, 187, 676, 677, 678, 681, 878, 909, 1093; AMNH locs. Elk Creek, Tenmile Creek, 3 miles S. of Shoshone R.; UCM locs. 84195, 84198; UW locs. 28, 34, 37, 38, 55 (Sandcouleean—early Graybullian, Willwood Fm.), Wyoming.

*Known distribution.*—Early Wasatchian (Sandcouleean—early Graybullian)—Bighorn Basin (Willwood Fm.) and Powder River Basin (“Wasatch Fm.”), Wyoming; earliest Wasatchian (Sandcouleean)—Four Mile area (Wasatch Fm.), Colorado.

*Discussion.*—*D. s.-primus* is the earliest known lineage segment of *D. secans* and the most primitive in features treated above in the diagnoses and discussions of the other lineage segments. Dentally, it is also the most primitive known artiodactyl. It is most distinct from the other lineage segments in lacking a postmetacristid on all known  $P_4$ s, and a talonid notch and a postmetacristid on the molars, and in having an unreduced molar paraconid directly anterior to the metaconid.  $P^3$  have a weak protocone either directly lingual to the paracone or slightly posterior; some have an incipient metacone on the post-paracrista near the metastyle.

Apart from its degree of morphologic overlap with *D. s.-metsiacus*, the most variable feature in *D. s.-primus* is the morphology of the hypocristid on  $M_3$ . On eight of the  $M_3$ s ( $n = 33$ ) the hypocristid divides into two forks, one of which extends to the hypoconulid and the other partly or completely to the entoconid. This feature also occurs on one  $M_3$  of *Artiodactyla* sp. A (UCM 47891;  $n = 11$ ), *Artiodactyla* sp. B, (CM 43133;  $n = 1$ ), *D. s.-metsiacus* (UCM 19427;  $n = 35$ ), *D. s.-kelleyi* (CM 22816;  $n = 47$ ) and one figured  $M_3$  of the European *D. gazini* (Sudre et al., 1983). Among non-diacodexoids, a partial or complete connection between the entoconid and hypoconid occurs in antiacodontids and homacodontids. Other derived characters shared by the latter clades (elevation of conjoined paraconid and metaconid on  $M_{1-3}$ ; non-inflation of metaconid; conical entoconid isolated from hypoconulid and as tall as the hypoconid; broad postcingulid; strong hypoconulid and hypocristid) do not occur in *D. s.-primus* but, in part, do

Table 10.—Dimensions of upper teeth of *Diacodexis secans*, lineage segment D. s.-primus.

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
AMNH 15671	10 Mile Cr	5.6	3.7	3.5	4.6	4.1	5.0	4.1	6.0	4.0	5.9
UCM 52579	UCM 84195	5.1		3.7	4.4	3.9	5.1	4.2	4.9		
CM 17467	CM 681			3.4	4.7	4.0	4.9				
UCM 38121	BHB			3.9	5.0	4.1	5.2	4.2	5.6	3.9	5.4
CM 36813	CM 878			4.0	4.5						
CM 12301	CM 676					3.9	5.0	4.4	5.7	4.6	6.0
CM 36814	CM 878					4.0	4.8	4.4	5.9	4.4	6.0
UW 9215	UW 38					4.2	4.8	4.6	5.8	4.3	6.0
CM 38865	CM 953					3.8	5.2				
CM 38865	CM 953					4.0	4.9				
CM 38865	CM 953					3.6	4.6				
CM 28974	CM 909					4.0	5.4				
CM 36175	CM 878					4.0					
CM 36179	CM 878					3.8	5.0				
CM 36210	CM 878					4.1	5.2				
CM 36809	CM 878					3.7	4.8				
CM 36801	CM 878					3.9	4.8				
CM 37438	CM 878					4.0	4.8				
UCM 49137	UCM 81002					3.8	5.4				
CM 28956	CM 157							4.5	6.2		

Table 10.—Continued.

Specimen no.	P <sup>3</sup>		P <sup>2</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
	L	W	L	W	L	W	L	W	L	W
	Locality									
CM 36211							4.5		5.8	
CM 36804							4.3		5.6	
CM 36816							4.3		5.4	
CM 37435							4.5		5.7	
UCM 49405							4.7		5.9	
CM 53709									5.8	
CM 38866							4.0		5.6	
CM 38866							4.0		5.3	
CM 38867							4.3		5.6	
CM 38869										
CM 38868										
CM 36177									3.5	5.0
CM 36208									4.0	5.1
CM 36602									4.1	5.6
CM 36808									4.2	5.5
CM 37439									4.0	5.8
CM 37439									4.5	5.7
CM 53724									4.5	5.5
CM 53724									3.8	5.2
Mean	3.70		4.64		3.94	5.01	4.33	5.68	4.14	5.59
N	5		5		18	16	15	16	13	13

describe the morphology of *Artiodactyla* sp. A and sp. B (see below) and some material of *D. s.-metsiacus*. As such, the frequency of occurrence of the partial or complete hypoconid-entoconid connection on  $M_3$  in *D. s.-primus* and *D. s.-metsiacus* may imply their ancestral position with regard to *Artiodactyla* sp. A and sp. B, antiacodontids and homacodontids. Such a conclusion agrees with the temporal occurrence of these taxa and, more importantly, with the retention of primitive features in antiacodontids and homacodontids (short  $P_{3-4}$ ; elongate hypoconulid lobe on  $M_3$ ; strong molar conules and conule-cristae) that are modified in more derived lineage segments of *D. secans*. Two upper molars of *D. s.-primus* from Four Mile are *Antiacodon*-like in the separation of the metaconule from the protocone, the deep trigon basin, the well-developed pseudohypocone, the strong conulecristae, and the nearly complete lingual cingulum.

*Diacodexis minutus*, new species

(Fig. 6; Tables 1-2, 11-12)

*Diacodexis chacensis*, Robinson, 1966:69.

*Diacodexis metsiacus*, Guthrie, 1971:85 in part.

*Etymology*.—*minutus*, L., small; in allusion to the small size of this species.

*Holotype*.—CM 22512, left  $P_4$ - $M_3$ , from CM loc. 34, Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

*Diagnosis*.—Smaller and less robust than the penecontemporaneous lineage segment of *D. secans* (*D. s.-secans*), and less robust and  $M_2$  smaller than *D. woltonensis*, with molar cusps (especially metaconid) much less inflated, talonid basins deeper, cristae and conules more distinct. Unlike *Artiodactyla* sp. A and sp. B and *D. gracilis*, molar trigonids not as compressed anteroposteriorly, lower molars with strong talonid notch and postmetacristid and with more inflated cusps; paraconid usually less medial and less reduced than in *D. gracilis*; metaconid-paraconid wall not as elevated as in *Artiodactyla* sp. A and sp. B.

*Syntypic series*.—CM 21132, 21142, 22538, 22593, 27475, 27459, 36443, 36446, 37311, 37313, 40765, 40769, 40774, 43712, 43713, 55138, 55152; UCM 46808; AMNH 17552, 92879, 96479; PU 13430.

*Referred specimens*.—CM 20982, 20989, 20992, 20994, 21000, 21013, 21075, 21098, 21129, 21130, 21132, 21142, 21928, 22538, 22593, 27459, 27460, 30953, 30989, 31002, 31010, 35786-35791, 36417, 36443, 36446, 37305, 37306, 37309-37313, 40765, 40767-40769, 40771, 40774, 40775, 42071, 42072, 42118, 43192, 43193, 43473, 43706, 43709, 43710, 43712, 43713, 44845, 44907, 44913, 55135-55139, 55152-55155, 55157, 55159, 55363, 55367; AMNH 17552, 92879, 94472, 96479; UCM 46808, 45516, 44401 (tentatively); PU 13430, 18344.

*Localities*.—AMNH loc. Huerfano 6 (Lostcabinian, Huerfano Fm.); CM loc. 1046, AMNH loc. Alkali Creek (Lostcabinian, Lost Cabin

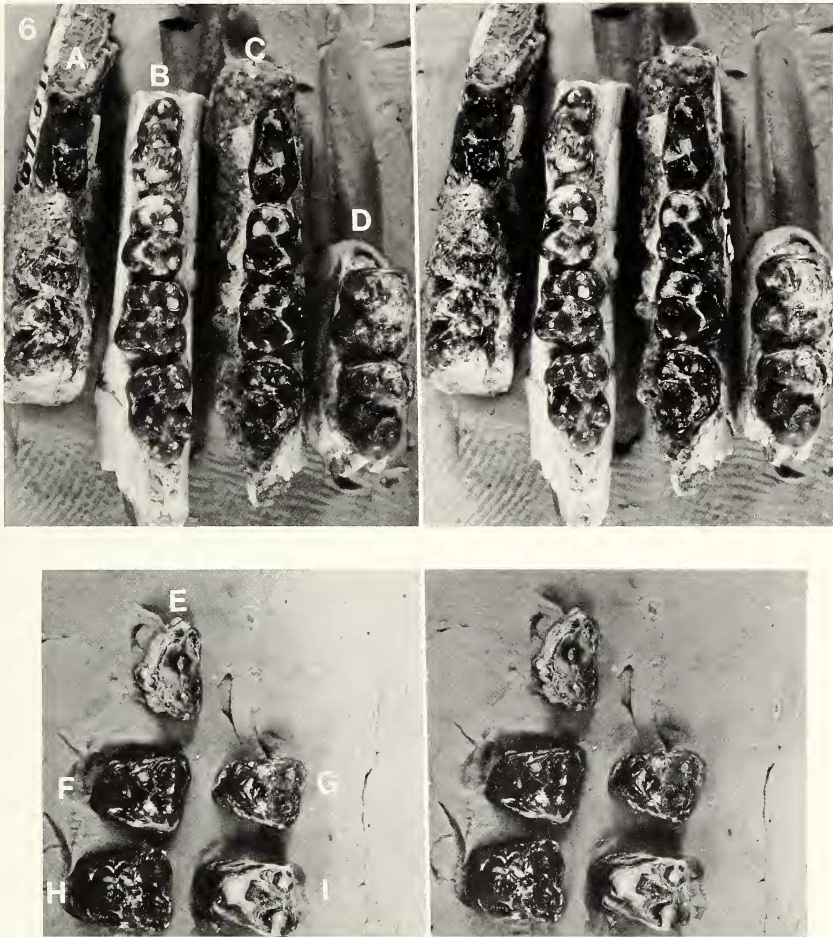


Fig. 6. — *Diacodexis minutus*, new species. (A) CM 40769; (B) CM 22512, holotype; (C) CM 55152; (D) CM 40774; showing range of variation in the lower teeth. (E) CM 44913, P<sup>3</sup>; (F) CM 55139, M<sup>1</sup>; (G) UCM 46808, M<sup>1</sup>; (H) UCM 44401, M<sup>2</sup>; (I) CM 43712, M<sup>2</sup>. All approx.  $\times 2$ .

Mbr., Wind River Fm.); UCM loc. 80062 (Lostcabinian, Red Creek facies, Wind River Fm.); CM locs. 34, 1036, 1078, UCM loc. 81027 (Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.).

*Known distribution.*—Late Wasatchian (Lostcabinian)—Huerfano Basin (Huerfano Fm.), Colorado; late Wasatchian to early Bridgerian



Table 11.—Dimensions of lower teeth of *Diacodexis minutus* from the Wind River Formation, Wyoming.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 43192	CM 34	5.2	1.7	4.7	2.1						
CM 21130	CM 34	5.4	2.0								
CM 37313	CM 34	5.0	1.8	4.2	2.4	3.7	2.8	3.8	3.4		
CM 37312	CM 34			4.7	2.5	4.0	3.1	4.0	3.6		
CM 22512*	CM 34			4.5	2.4						
CM 22512*	CM 34			4.7	2.8	3.8		3.9	3.3	4.9	3.1
CM 43473	CM 34			4.5	2.5						
CM 55136	CM 34			4.2	2.3						
CM 55363	CM 34			4.8	2.6						
CM 55137	CM 34			4.7	2.5	3.8	3.2				
CM 21129	CM 34			4.8	2.6						
CM 21013	CM 34			4.6	2.5						
CM 40767	CM 34			4.7	2.6	3.6	3.0	4.0	3.4		
CM 40769	CM 34			4.7	2.5	3.1	4.0	4.0	3.5		
CM 20989	CM 34			4.2	2.3	3.8	3.0	3.8	3.4		
CM 21000	CM 34			4.6	2.5	3.8	3.1				
CM 20982	CM 34			4.4	2.3	3.7					
CM 43193	CM 1078			4.1	2.0						
CM 30989	CM 34			5.0	2.8						
CM 27459	CM 34			4.7	2.7	3.7	3.1	4.0	3.2		
CM 55152	CM 34			4.6	2.5	3.7	2.9	3.8	3.1	4.5	3.2
AMNH 17552	Huerfano 6			4.2	2.1	4.0	3.0	4.4	3.5		
AMNH 92879	CM 1046			4.5	2.5			4.2	3.5	4.8	3.2
PU 13430	CM 34			4.8	2.7	4.1	3.3	4.1	3.5		
PU 18344	CM 34					3.8	3.0	3.9	3.1		
CM 55157	CM 34			3.7	3.0	3.7	3.0	3.7	3.1	4.7	3.2
CM 55153	CM 34			3.9	3.3						
CM 55367	CM 34			4.0	3.0	4.0	3.0	3.9	3.3		
CM 55159	CM 34			3.8	3.1	3.8	3.1				
CM 55155	CM 34			4.4	3.5						

Table 11.—Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 42071	CM 34					3.9	2.8				
CM 37311	CM 34						3.1	4.0	3.4		
CM 37306	CM 34			4.0			3.3				
CM 44914	CM 34			3.8			3.0				
CM 40765	CM 34			3.8			3.0	4.2	3.5		
CM 31002	CM 34			3.7			3.1	3.8	3.5	4.9	3.2
CM 22538	CM 34			4.1			3.1				
CM 42118	CM 34			3.9			3.0				
CM 43710	CM 34			3.8			3.0				
AMNH 96479	Alkali Cr.			3.7			2.6				
CM 42072	CM 34						4.1	4.1	3.4	4.9	3.4
CM 30953	CM 34						4.1	4.1	3.2		
CM 37309	CM 34						4.1	4.1	3.6	5.1	3.5
CM 21132	CM 34						4.2	4.2	3.3		
CM 40774	CM 34						4.3	4.3	3.5	4.8	3.1
CM 40771	CM 34						4.0	4.0	3.4	4.6	3.2
CM 40768	CM 34						3.8	3.8	3.4	4.6	3.2
CM 21142	CM 34						3.8	3.8	3.2	4.6	3.0
CM 36417	CM 34						4.2	4.2	3.5		
CM 40775	CM 34						3.9	3.9	3.3	4.8	3.0
AMNH 94472	Huerfano 6						4.4	4.4	3.5		
CM 43706	CM 34						4.0	4.0	3.5	5.4	3.5
CM 31010	CM 34						3.9	3.9	3.4	4.8	3.1
CM 27460	CM 34						3.8	3.8	3.6	4.8	3.2
CM 20994	CM 34						3.5	3.5	3.5	4.8	3.1
CM 55135	CM 34						4.2	4.2	3.3		
CM 55138	CM 34						4.2	4.2	3.6	5.0	3.6
CM 22593	CM 34						4.2	4.2	3.3	4.8	3.4
CM 21075	CM 34									4.9	3.1

Table 11. —Continued.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
CM 21928	CM 34									4.8	3.2
CM 43709	CM 34									5.0	3.3
CM 44845	CM 1036									4.7	3.1
CM 21098	CM 34									4.9	3.1
CM 37305	CM 34									4.6	3.5
CM 35791	CM 34									4.7	2.9
CM 20992	CM 34									5.0	3.4
Mean		5.20	1.83	4.56	2.47	3.85	3.06	4.02	3.40	4.82	3.22
N		3	3	23	23	27	27	34	34	26	27

\* Holotype of *D. minutus*.

(Lostcabinian—Gardnerbuttean)—Wind River Basin (Wind River Fm.), Wyoming.

*Discussion.*— $P^4$  and teeth anterior to  $P^3/3$  are unknown. The dentition of *D. minutus* is smaller and more gracile than that of *D. s.-secans*, *D. s.-primus*, most specimens of *D. s.-kelleyi* and *D. woltonensis*, and many specimens of *D. s.-metsiacus*. It is closest in size to some specimens of *D. s.-metsiacus*, *Artiodactyla* sp. A, *D. gracilis*, and three specimens of *D. s.-kelleyi*, but can be distinguished from these groups by the following suite of features: elongate  $P_3$ ; strong postmetacristid on  $P_4$ – $M_3$ ; deep talonid basin and well-developed talonid notch on  $M_{1-3}$ . Additionally, the molar trigonids are not as compressed antero-posteriorly as in *Artiodactyla* sp. A and *D. gracilis*, the paraconid is not as reduced and medial as in *D. gracilis*, and the trigonid not as elevated as in *Artiodactyla* sp. A.

*D. minutus* occurs penecontemporaneously and in lithosympatry in the Lostcabinian with *D. s.-secans* and *D. woltonensis* and in lithosympatry with *D. s.-secans* at the Gardnerbuttean CM loc. 34. Compared to these groups, the teeth in *D. minutus* are smaller,  $P_4$  almost invariably has a postmetacristid,  $M_{1-2}$  are less nearly square, the molar metaconids are usually much less inflated, the protoconids and hypoconids are less bulbous, the talonid basins are deeper and the hypoconulid and entoconid often share a common wall. Derived features shared with *D. s.-secans* and *D. woltonensis* are the high frequency of occurrence of a well-developed molar postmetacristid and talonid notch; these morphoclineal features may imply the common ancestry of *D. s.-secans*, *D. woltonensis* and *D. minutus* from *D. s.-kelleyi*, specimens of which approach and overlap the former taxa in these features. Indeed, three of the smallest specimens assigned to *D. s.-kelleyi* (CM 39221; 54212, 44906) may represent either Lysitean *D. minutus* or that part of the variation of *D. s.-kelleyi* that was canalized in *D. minutus*. Other derived (and morphoclineal) features, such as robusticity of the molars (especially the metaconid) also link *D. s.-secans* and *D. woltonensis* with *D. s.-kelleyi*.

Alternatively, *D. minutus* may be more closely related to the *D. s.-metsiacus* segment of the *D. secans* lineage, molars of which also bear a postmetacristid and talonid notch (although they are weaker and occur at a lower frequency) as well as a more gracile metaconid (some specimens), as in *D. minutus*.

The problem of reconstructing the specific evolutionary relationships of *D. minutus* is grounded in the non-digital nature of the derived character states, namely, a series of temporal morphoclines that first appear in *D. s.-metsiacus*, increase in the frequency and degree of expression in *D. s.-kelleyi*, and more so in *D. s.-secans*, *D. woltonensis*,

Table 12.—Dimensions of lower teeth of *Artiodactyla* sp. A, *Artiodactyla* sp. B, and *Diacodexis gracilis*.

Specimen no.	Locality	P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W	L	W
<i>Artiodactyla</i> sp. A											
CM 43135	CM 941		1.5	4.9	2.1						
CM 43129	CM 945			4.5	2.1						
UCM 48526	UCM 78049			4.1	2.3	3.7		4.0	3.4	4.8	2.8
UCM 47053	UCM 78049							4.0	3.3		
CM 43132	CM 941							4.1	3.2		
CM 10475	Indian							4.2	3.5	5.1	3.1
CM 10475	Valley					4.2		4.2	3.3		
CM 43702	Scenery							4.2	3.4	4.8	3.2
	Gulch										
CM 43130	CM 1017									5.2	3.2
UCM 47052	UCM 78049							4.2	3.6	4.9	3.3
AMNH 16296	Ojo San Jose							4.3	3.4	5.2	3.1
	E. Bluff										
CM 43134	CM 1017									4.7	2.9
UCM 47891	UCM 78049									5.0	3.1
UCM 40831	UCM 78033									5.0	3.1
Mean				4.50	2.17	3.95	2.80	4.14	3.39	4.97	3.09
N				3	3	2	5	7	8	9	9
<i>Artiodactyla</i> sp. B											
CM 43133	CM 941					4.4	3.2	5.0	3.7	6.4	3.6
CM 43128	CM 941							4.8	3.2		
AMNH 237	GGG 1949							4.7	3.7	6.2	3.6
AMNH 86289	GGG 1937							4.7	3.7	5.9	3.7
Mean								4.83	3.53	6.17	3.63
<i>Diacodexis gracilis</i>											
UCM 52582*	UCM 84255			4.0	2.2	3.8	2.8	3.7	3.8	4.8	3.0
UCM 52583	UCM 84180			3.9	2.3	3.7	2.8	3.9	3.3		
UCM 52584	UCM 84250					3.8	2.8	3.9	3.3	4.5	3.0
Mean				3.95	2.25	3.77	2.80	3.83	3.47	4.65	3.00

\* Holotype.



and *D. minutus*. Furthermore, each of these characters varies continuously in *D. s.-metsiacus* and *D. s.-kelleyi*. As such, there are two acceptable conclusions: (1) *D. minutus* shared an immediate common ancestry with *D. s.-secans* and *D. woltonensis* from *D. s.-kelleyi*, in which case the terminal expression of the morphoclines in the three descendant groups is due to direct descent; (2) *D. minutus* shared an immediate common ancestry with *D. s.-kelleyi* from *D. s.-metsiacus*, in which case the terminal expression of the morphoclines in *D. minutus* on the one hand and *D. s.-secans* and *D. woltonensis* on the other are due to parallelism. Lower molars of *D. s.-secans* and *D. woltonensis* bear greatly inflated metaconids (the terminal expression of another morphocline). The metaconid is usually gracile in *D. minutus*, but is inflated in some Gardnerbuttean specimens (CM 40765, 22593, 22538, 40769, 40774) of this species and approaches the condition in *D. woltonensis* and some Gardnerbuttean specimens of *D. s.-secans* (especially CM 22504). Similarly, the degree of inflation of the molar metaconid is variable in *D. s.-kelleyi* and overlaps at the extremes of the distribution with *D. minutus* on the one hand and *D. s.-secans* and *D. woltonensis* on the other. Such a pattern of variation can also imply either parallelism or direct descent. In sum *D. minutus*, *D. woltonensis*, and *D. s.-secans* appear to have shared a common ancestry from either the same (*D. s.-kelleyi*) or two different lineage segments (*D. s.-metsiacus*, *D. s.-kelleyi*) of *D. secans*. This kind and degree of variation in evolving morphoclines has been noted in other taxa with a good fossil record (Gingerich and Simons, 1977).

Two other variable features of note in *D. minutus* are the position and strength of the molar paraconid and the presence of a metaconid on P<sub>4</sub>. The paraconid on M<sub>1-3</sub> is usually small and slightly medial relative to the metaconid, but can be much reduced (M<sub>3</sub> in CM 20992, 22593; M<sub>1-2</sub> in CM 21132) and quite medial (M<sub>2</sub> in CM 37311, 37312). The metaconid, absent on all but two P<sub>4</sub>s, is almost as strong as the protoconid on CM 55152 and is incipient on CM 40769. One M<sub>1</sub> (CM 22538) is unique in having a fused entoconid and hypoconulid.

The few known upper molars of *D. minutus* are much smaller and less robust than those of *D. s.-secans* and most specimens of *D. s.-kelleyi*, and more closely resemble those of *D. s.-metsiacus* in the lack of inflation of the protocone and conules, and the more distinct conulecristae and pseudohypocone. Premetaconulecristae are usually weak or absent.

One specimen of *D. minutus* (CM 44907) preserves a fused distal tibia and fibula. This condition is not surprising, given its occurrence in the more primitive *D. secans* (lineage segment *D. s.-metsiacus*; Rose, 1982), and other apparent sister taxa of the latter—leptochoerids, antiacodontids, and homacodontids. It should also occur in more derived lineage segments of *D. secans* and in *D. woltonensis*.



Fig. 7.—*Diacodexis woltonensis*, new species. (A) CM 43474; (B) CM 43478, holotype; both approx.  $\times 2$ .

*Diacodexis woltonensis*, new species  
(Fig. 7; Tables 1, 13)

*Diacodexis metsiacus*, Guthrie, 1971:85, in part.

*Etymology*.—After the now extinct village of Wolton, Wyoming, near Alkali Creek in the Wind River Basin.

*Holotype*.—CM 43478, right  $P_4$ – $M_3$ , from CM loc. 1077, Lost Cabin Member, Wind River Formation, Wyoming.

*Diagnosis*.—Most robust species of *Diacodexis* in proportion to size, with nearly square  $M_{1-2}$ , hyperinflated metaconid, swollen protoconid and hypoconid, small talonid basin; additionally differs from *D. gracilis* and *Artiodactyla* sp. A and sp. B in having a strong talonid notch and postmetacristid on the lower molars, and a non-compressed trigonid.

*Syntypic series and referred specimens*.—CM 22592, 40783, 42090–42092, 43474; AMNH 92871; UCM 44423, 44696, 46810.

*Localities*.—CM locs. 91, 1041, 1042, 1046, 1077 (Lostcabinian, Lost Cabin Mbr., Wind River Fm.); UCM loc. 80062 (Lostcabinian, Red Creek Facies, Wind River Fm.).

*Known distribution*.—Late Wasatchian (Lostcabinian)—Wind River Basin (Wind River Fm.), Wyoming.

*Discussion*.—*D. woltonensis* occurs in lithosympatry with *D. s.-secans* (at many localities) and *D. minutus* (at one locality) in the Lost-

Table 13.—Dimensions of lower teeth of *Diacodexis woltonensis* from the Wind River Formation, Wyoming.

Specimen no.	Locality	P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>	
		L	W	L	W	L	W	L	W
CM 42092	CM 1041		2.4	5.0	2.8				
CM 42090	CM 1042			5.5	3.1				
CM 42090	CM 1042			5.7	3.1			5.6	3.9
CM 43474	CM 1046			5.3	2.7			4.2	3.7
CM 43478*	CM 1077			5.1	2.6	4.0	3.2	4.2	3.7
AMNH 92871	WRB			5.5	2.7	4.2	3.3	4.2	3.7
CM 40783	CM 1041					4.3	3.4	4.2	4.0
UCM 44423	UCM 80062					4.0	3.4		
UCM 44696	UCM 80062					4.2	3.3		
CM 42091	CM 1041							4.3	3.8
CM 22592	CM 91							4.1	3.5
UCM 46810	UCM 80062							4.21	3.76
Mean				5.35	2.83	4.14	3.32	4.21	3.76
N				6	6	5	5	7	7

\* Holotype.

cabinian part of the Wind River Basin, where it is smaller (no overlap) than the former and much more robust and slightly larger (mean size) than the latter (Fig. 13). Specifically,  $M_{1-3}$  of *D. woltonensis*, unlike *D. minutus*, bear a hyperinflated metaconid, swollen protoconid and hypoconid, a larger hypoconulid, and a smaller talonid basin. Like *D. s.-secans* and *D. minutus*, lower molars of *D. woltonensis* have a strong postmetacristid and talonid notch, features which, as discussed above (see *D. minutus*), may imply their common ancestry from *D. s.-kelleyi* or may have developed in parallel in *D. minutus* from *D. s.-metsiacus*. In either case, these derived features, as well as the increased robusticity of the molars, are shared by *D. woltonensis* and *D. s.-secans* and imply their common ancestry from *D. s.-kelleyi*.

Although Lostcabinian samples of *D. woltonensis*, *D. minutus*, and *D. s.-secans* are discrete, Lostcabinian *D. woltonensis* overlaps in size and robusticity of the lower molars and inflation of the metaconid with a few specimens of both Gardnerbuttean *D. minutus* (CM 40774, 40769) and *D. s.-secans* (especially CM 22504) from CM loc. 34. Importantly, these specimens comprise, respectively, the upper and lower extremes of the normal distribution of these two species; also, the mean size of Lostcabinian *D. woltonensis* is intermediate between that of Gardnerbuttean *D. minutus* and *D. s.-secans*.

Our recognition of *D. woltonensis* as a discrete species is based on its clear morphological distinction from lithosympatric Lostcabinian samples of *D. s.-secans* and penecontemporaneous (and lithosympatric) samples of *D. minutus*. Given this systematic interpretation, the pattern of morphological overlap in the Gardnerbuttean may be explained by the local extinction of *D. woltonensis* and consequent expansion of the range of variation of *D. minutus* and *D. s.-secans* toward the size and robusticity of *D. woltonensis*. Other systematic interpretations of the Lostcabinian and Gardnerbuttean material are possible, and may become more evident and tenable with a larger sample size of *Diacodexis*, especially from the Lostcabinian. For example, the Lostcabinian material referred to *D. minutus* may represent the more gracile part of the range of variation of *D. woltonensis*. Alternatively, *D. woltonensis* may represent the more robust part of the range of variation of Lostcabinian *D. minutus*. The few Gardnerbuttean specimens of *D. minutus* and *D. s.-secans* that closely resemble Lostcabinian *D. woltonensis* may represent that species. Any of these hypotheses, if corroborated by further collecting, would alter our reconstruction of the relationships of these taxa. However, the current record and its morphological patterns support the recognition and co-occurrence of three species of *Diacodexis* in the Lostcabinian and two in the Gardnerbuttean.

Variable features in *D. woltonensis* include size of  $M_3$ , and develop-



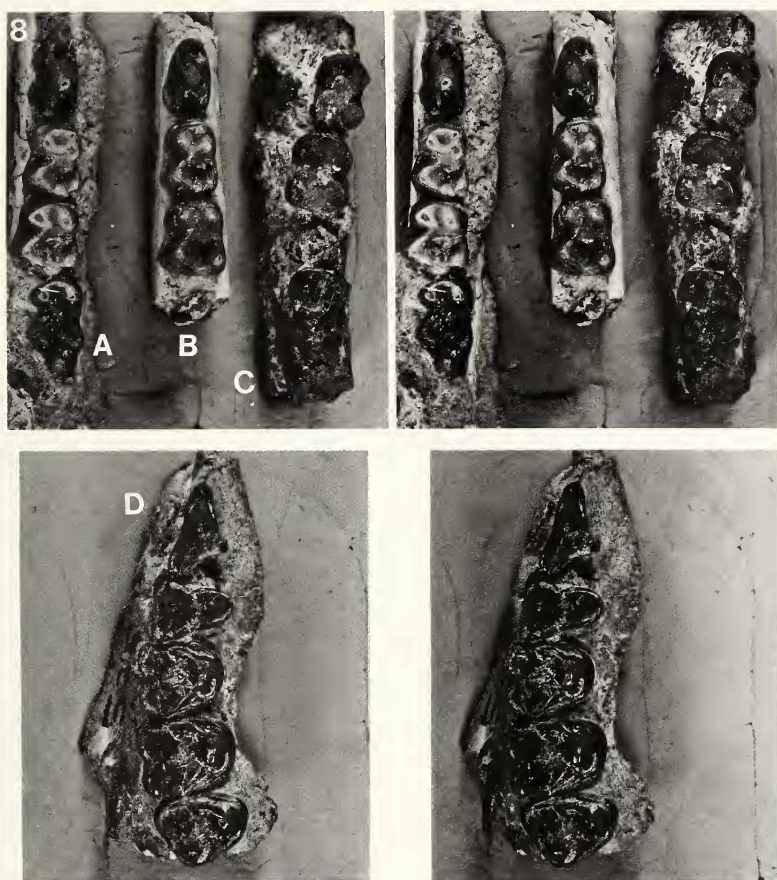


Fig. 8.—*Diacodexis gracilis*, new species. (A) UCM 52582, holotype; (B) UCM 52583; (C) UCM 52584; (D) UCM 52585; all approx.  $\times 2$ .

ment of the paraconid on the lower molars and especially  $P_4$ , where it can be extremely weak or as large as in *D. secans* and *D. minutus*.

*Diacodexis gracilis*, new species, Krishtalka, Stucky, and Bakker  
(Fig. 8; Tables 1–2, 12, 14)

*Etymology*.—*gracilis*, L., in allusion to the gracile morphology of the dentition.

*Holotype*.—UCM 52582, left  $P_4$ – $M_3$ , from UCM loc. 84255, Willwood Formation, Bighorn Basin, Wyoming.

*Diagnosis*.—Smallest and most gracile species of *Diacodexis*, with most reduced and medial paraconid on  $M_{2-3}$ , most gracile metaconid



Table 14.—Dimensions of upper teeth of *Artiodactyla* sp. A, *Diacodexis gracilis*, and *Diacodexis minutus*.

Specimen no.	Locality	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>	
		L	W	L	W	L	W	L	W	L	W
<i>Artiodactyla</i> sp. A											
UCM 47889	UCM 78049			3.7	4.4	4.2	5.7	3.4	5.5		
UCM 48517	UCM 78049			3.6	4.8						
CM 43138	CM 941			3.9	5.0	4.1	5.6	4.1	6.3		
CM 43131	CM 941					4.5	6.0	4.1	6.3		
UCM 47054	UCM 78049					3.7	5.4				
Mean				3.73	4.73	4.13	5.68	3.75	5.90		
<i>Diacodexis gracilis</i>											
UCM 52585	UCM 84256	4.8	2.5	3.6	4.2	3.9	4.8	3.5	4.4		
<i>Diacodexis minutus</i>											
CM 44913	CM 34	4.6	3.1								
CM 35786	CM 34			3.7	5.2						
CM 55139	CM 34			3.7	4.7						
CM 43712	CM 34			3.5	5.0						
UCM 44516	CM 34			3.2	4.7						
UCM 46808	UCM 81027			3.5	4.5						
UCM 44401	UCM 80062					4.0	5.0				
CM 35787	CM 34						5.5				
CM 35789	CM 34						5.9				
CM 36446	CM 34					3.9	5.0				
CM 37310	CM 34					3.6	5.2				
CM 55154	CM 34					3.7	5.1				
CM 36443	CM 34					3.9	5.3				
CM 43713	CM 34					4.0	5.1				
Mean				3.52	4.82	3.85	5.26				
N				5	5	6	8				

and compressed trigonid on  $M_{1-3}$ , and with metacone (weak) on  $P^4$ ; additionally, differs from all species of *Diacodexis* (except *D. secans* lineage segment *D. s.-primus*) in lacking a postmetacristid and talonid notch on  $M_{1-3}$ .

*Syntypic series and referred specimens.*—UCM 52583–52585.

*Localities.*—UCM locs. 84180, 84250, 84255, 84256 (late Graybullian, Willwood Fm.), Bighorn Basin, Wyoming.

*Known distribution.*—Early Wasatchian (late Graybullian)—Bighorn Basin (Willwood Fm.), Wyoming.

*Description.*—Teeth anterior to  $P^3$  and  $P_4$  are unknown.  $P_4$  is short and bears a double paraconid and a postmetacristid. Unlike  $M_1$ , the trigonid is compressed on  $M_{2-3}$  and the paraconid is severely reduced and more medial. Postmetacristids and talonid notches are absent and the metaconids are uninflated.  $P^3$  is triangular in occlusal view, with a weak protocone offset posteriorly.  $P^{3-4}$  bear a weak metacone at the midpoint of the postparacrista, and a somewhat elongate, sharply pointed parastyle.  $M^{1-3}$  are uninflated, have sharp cusps, conules, and cristae, and perhaps the most distinct pseudohypocones among species of *Diacodexis*.

*Discussion.*—*D. gracilis* most closely resembles the *D. s.-metsiacus* lineage segment of *D. secans* in overall dental morphology, but is slightly smaller, has a more compressed trigonid and a more reduced and medial paraconid on  $M_{2-3}$ , and a slightly less inflated metaconid on  $M_{1-3}$ . It also differs from *D. minutus* in these features as well as in lacking a postmetacristid and talonid notch on  $M_{1-3}$ , and in having a much less inflated metaconid. Although there is no morphologic overlap between *D. gracilis* and these groups, some specimens of *D. s.-metsiacus*, *D. minutus*, and *Artiodactyla* sp. A approach the *D. gracilis* condition in isolated features. On a few molars of *D. minutus* (CM 21132, 22593, 37311, 37312) the paraconid is either nearly as weak or as medial as in *D. gracilis*, but the molars otherwise differ from the latter as described above. Similarly, the paraconid on some specimens of *Artiodactyla* sp. A is small, but never as reduced or as medial as in *D. gracilis*. The known material suggests that *D. gracilis* is most closely related to *D. s.-metsiacus* and independently evolved a reduced, more medial paraconid on  $M_{2-3}$  and a more compressed trigonid on  $M_{1-3}$ . It lacks the more derived character states of *Artiodactyla* sp. A and sp. B, *D. minutus*, *D. woltonensis*, and more evolved lineage segments of *D. secans*. Among known species of *Diacodexis*, *D. gracilis* exhibits the least amount of gradational difference from its putative ancestor. This may be due to small sample size (four specimens).

#### ***Artiodactyla* sp. A (or spp.)**

(Tables 1–2, 12, 14)

*Diacodexis metsiacus*, Kihm, 1984.

*Referred specimens.*—CM 43129–43132, 43134–43136, 43138; AMNH 16296—from the San Jose Fm. (late Graybullian–Lysitean), San Juan Basin, New Mexico. CM 10475,

43702; UCM 40831, 47052–47054, 47889, 47891, 48517, 48526—from the Debeque Fm. (late Graybullian–Lysitean), Piceance Basin, Colorado.

*Discussion.*—This small sample of artiodactyls from the San Juan and Piceance basins may represent one or two species of *Diacodexis* or a new genus. More material is needed for a systematic resolution of this sample. The lower molars have an uninflated metaconid, an elevated and conjoined paraconid and metaconid, a small paraconid anterior or barely anteromedial to the metaconid, an elongate talonid (most specimens), a broad postcingulid, and a lingual hypoconulid isolated from a conical entoconid, which is equal in height to the hypoconid in most specimens. The lower molars lack a postmetacristid and a talonid notch, but the talonid basin is open lingually due to the absence of a pre-entocristid. These features, in part, define the derived condition of antiacodontids and homacodontids and become further developed in these clades. The lower molars also lack the other specializations that define the most primitive known antiacodontid (*Antiacodon*, new species, Lostcabinian, Bighorn Basin), and homacodontid (*Hexacodus uintensis*, Lysitean–Lostcabinian, Wind River and Green River basins; Stucky and Krishtalka, manuscript).

P<sub>3</sub> is shorter than P<sub>4</sub>. Both are gracile, lack a postmetacristid, and have a posterior trigonid wall that is concave, as in antiacodontids and homacodontids.

The upper molars are variable in the presence of a weak but distinct mesostylar flexure, which on CM 43138 (M<sup>1-2</sup>) is formed by an extension of the premetacrista dorsally beyond the apex of the centrocrista to the ectocingulum. On M<sup>3</sup> (but not M<sup>2</sup>) in CM 43131 and UCM 47889, the apex of the centrocrista has a slight labial flexure, which is not an extension of the premetacrista and does not reach the ectocingulum. The other upper molars in this sample (UCM 47054, M<sup>2</sup>; UCM 48517, M<sup>1</sup>) lack a mesostyle.

Both mesostylar conditions, as well as other mesostylar variations occur in homacodontids and antiacodontids. The second condition (on M<sup>3</sup> in CM 43131, UCM 47889) also occurs on two M<sup>2</sup>s and all but one M<sup>3</sup> of *D. s.-kelleyi*; CM 43131 also resembles *D. s.-kelleyi* in the lingual distention of the periconal and hypoconal areas of the crown, and may represent the latter lineage segment of *D. secans* in the San Juan Basin. However, none of the lower molars in this sample is *D. s.-kelleyi*-like; the range of variation in the lower molars, as in the uppers, approaches the *D. s.-metsiacus* lineage segment of *D. secans* on the one hand, and antiacodontids and homacodontids on the other.

The lower premolars and some of the upper and lower molars in this sample from the San Juan and Piceance basins (CM 43129, 43135, 43138, 10475, 43132, 43134, 43136, 43130) seem more closely allied



Fig. 9.—Chronoclineal shifts in morphology in the lower dentition of *Diacodexis secans* from the Sandcouleean to the Gardnerbuttean (A to D). (A) Lineage segment *D. s.-primus* (AMNH 15672); (B) lineage segment *D. s.-metstiacus* (AMNH 15666); (C) lineage segment *D. s.-kelleyi* (CM 39880); (D) lineage segment *D. s.-secans* (UCM 42199); all approx.  $\times 2$ .

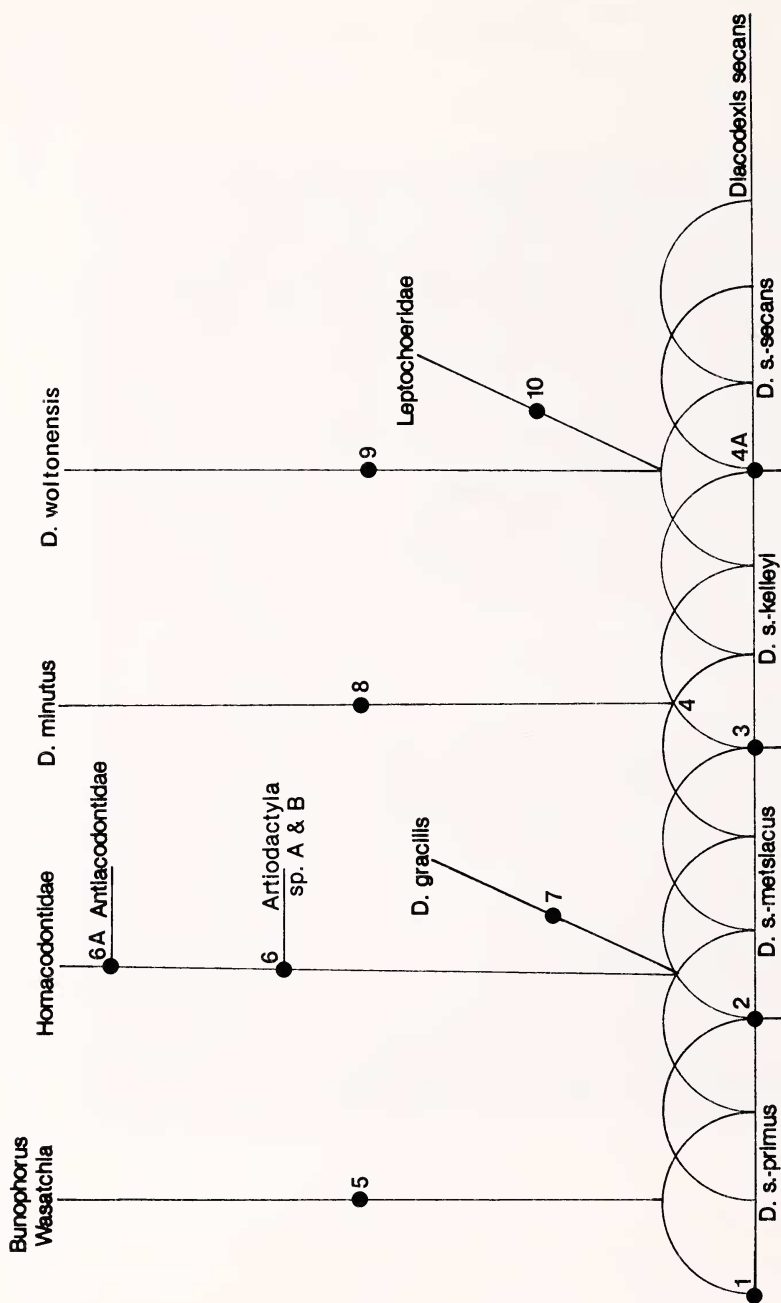


Fig. 10.—Phylogenetic relationships of *Diacodexis*, *Artiodactyla* sp. A, *Artiodactyla* sp. B, the *Wasatchia*-*Bunophorus* clade, *Antiactodontidae*, *Homacodontidae*, and *Leptochoeridae*. See text (conclusions) for an explanation of the derived characters at each node. Semi-circles denote anagenetic change and overlap in the frequency and expression of derived features in *Diacodexis secans*.



with homacodontids and antiacodontids than any known species of *Diacodexis*. Other specimens in this sample (AMNH 16296; UCM 40831, 47052–47054, 47889, 47891, 48517, 48526) are also similar to most specimens of *D. s.-metsiacus*, in having a short, wide  $M_{2-3}$  talonid, a nearly square  $M_2$ , and slightly inflated cusps. All of the material referred here exhibits the elevated trigonid, the conical, high entoconid, the small anterolingual paraconid conjoined with the metaconid and the broad postcingulid that imply affinity with antiacodontids and homacodontids. All of these characters appear to be continuously variable within this group, which may represent one or two new and derived species of *Diacodexis* or a new genus, or, less likely, a geographic subspecies of *D. secans*. Whatever the systematic resolution, which awaits a larger sample from the southwestern basins, this group is morphologically intermediate between *D. secans* and the homacodontid-antiacodontid clade. The current record implies that the radiation of this clade began in the southern and western basins in the early Eocene.

### **Artiodactyla sp. B**

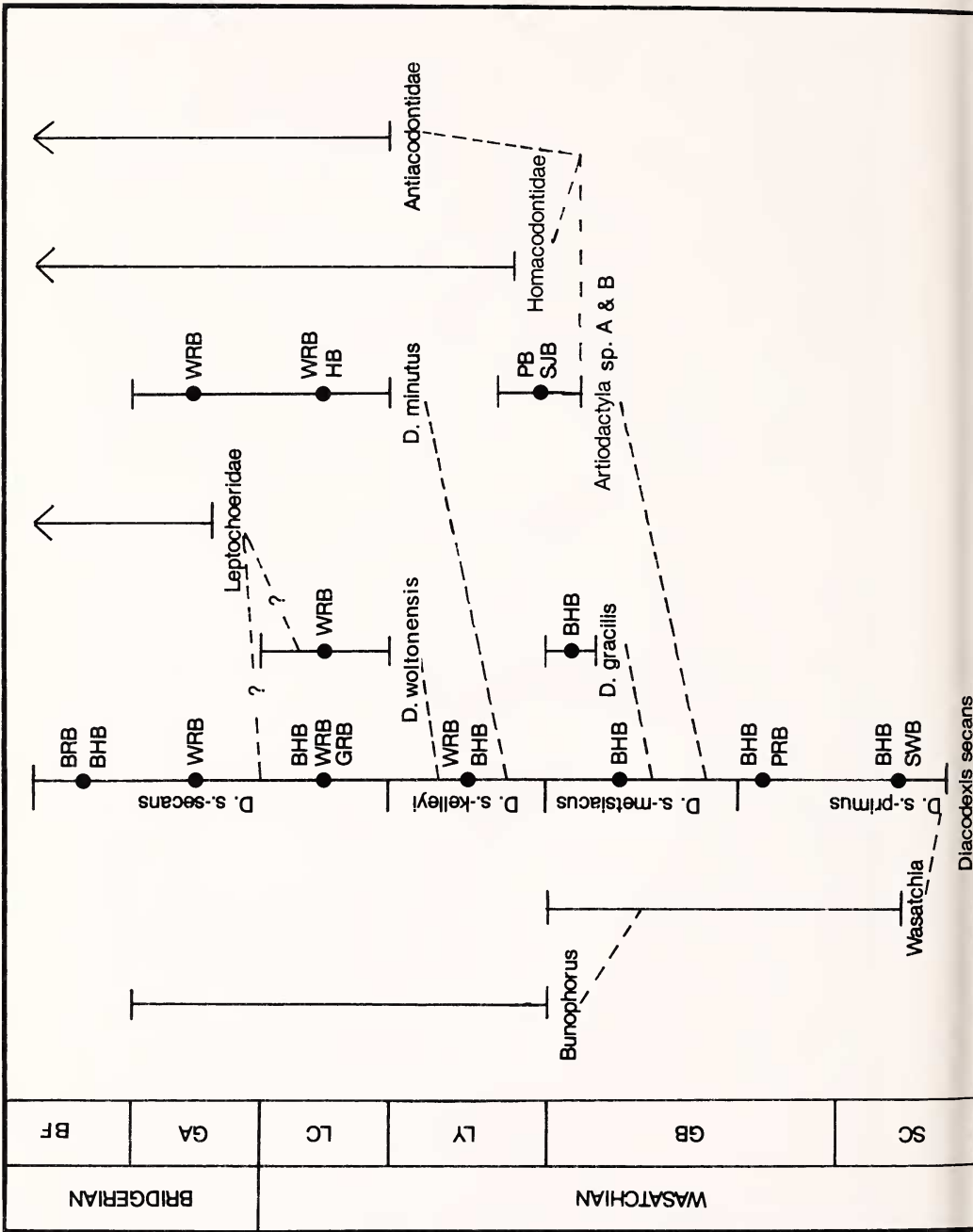
(Tables 1, 14)

*Referred specimens.*—CM 43128, 43133; AMNH 237, 86289—from the San Jose Fm. (late Graybullian–Lysitean), San Juan Basin, New Mexico.

These four specimens are larger, but otherwise virtually identical to *Artiodactyla* sp. A, especially those specimens that more closely resemble antiacodontids and homacodontids.

### CONCLUSIONS

Three species of *Diacodexis* occur in the Wind River Formation in the northeastern and central parts of the Wind River Basin—*D. secans*, *D. minutus* and *D. woltonensis*. *D. secans* includes as synonyms *D. metsiacus*, *D. brachystomus*, *D. laticuneus*, and *D. olseni*, and also occurs in the Bighorn, Green River, and Powder River basins, Wyoming, and the Sand Wash Basin (Four Mile area), Colorado. *D. secans* is known from Sandcouleean (earliest Wasatchian) through Blacksforkian (middle Bridgerian) horizons, and is divided into four, informal, temporally successive lineage segments (*D. s.-primus*, *D. s.-metsiacus*, *D. s.-kelleyi*, *D. s.-secans*) to reflect stages in its anagenetic evolutionary history (Figs. 9–11). In the Wind River Basin *D. secans* is represented by *D. s.-kelleyi* in the Lysite Member (Lysitean) and *D. s.-secans* in the Lost Cabin Member (Lostcabinian–Gardnerbuttean). *D. minutus* and *D. woltonensis* are new species; both co-occur with *D. secans* in the Lostcabinian, as does the former in the Gardnerbuttean (Figs. 12, 13). Other diacodexineans and allied taxa discussed here are unknown



from the Wind River Basin—*D. gracilis*, new species, from the late Graybullian of the Bighorn Basin; and *Artiodactyla* sp. A and sp. B, from the middle Wasatchian of the Piceance and San Juan basins. Recognition of all of these species is based primarily on non-meristic morphological features and, in certain instances, on differences in size.

*D. secans* is the main species-lineage of diacodexeines and appears to have been ancestral at different points in its anagenetic history to all other species of *Diacodexis*, as well as *Artiodactyla* sp. A and sp. B, the *Wasatchia-Bunophorus* clade, homacodontids, antiacodontids, and leptchoerids. Evolution within *D. secans* involved the chronocline increase in degree and frequency of expression of a number of derived morphological features (see diagnosis of each lineage segment and pp. 421–422 for summary). Morphocline evolution and canalization of derived traits also characterized the cladogenetic appearance of *D. woltonensis*, *D. minutus*, and *Artiodactyla* sp. A. Depiction of such morphocline continua in a cladogram of strictly dichotomous relationships based on derived, digital character states is not possible. We present a cladogram-like figure (Fig. 10) as a synopsis of diacodexeine relationships, with the following warnings: (1) It is not dichotomous. (2) Most of the nodes involve derived morphocline characters rather than digital ones; also, the species and lineage segments exhibit internal and continuous variation; thus, not every specimen assigned to a species or lineage segment bears every derived character at that node to the same degree. (3) Sister species approach and, in some instances, show partial morphologic overlap with one another in derived features, which, in our opinion, reflects the real and fuzzy boundaries between some species, given an adequate fossil record. This reconstruction of relationships among diacodexeines and allied taxa is based both on the determination and integrity of species in the fossil record, and the pattern of shared-derived morphological features among them. Besides the well-known phylogenetic principles of plesiomorphy and apomorphy, application of the too oft forgotten principle of “variamorphy,” or variation, is also required.

*D. secans* lineage segment *D. s.-primus* (Fig. 10, node 1) represents the primitive condition, from which the *Wasatchia-Bunophorus* clade

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←  
 Fig. 11.—Phylogenetic relationships and known occurrence (diagramatic) of the species of *Diacodexis*, *Artiodactyla* sp. A, and *Artiodactyla* sp. B. Abbreviations are: Land Mammal Sub-ages—SC, Sandcouleean; GB, Graybullian; LY, Lysitean; LC, Lostcabinian; GA, Gardnerbuttean; BF, Blackforkian. Basins—BHB, Bighorn Basin; BRB, Bridger Basin; GRB, Green River Basin; HB, Huerfano Basin; PB, Piceance Basin; PRB, Powder River Basin; SJB, San Juan Basin; SWB, Sand Wash Basin; WRB, Wind River Basin.

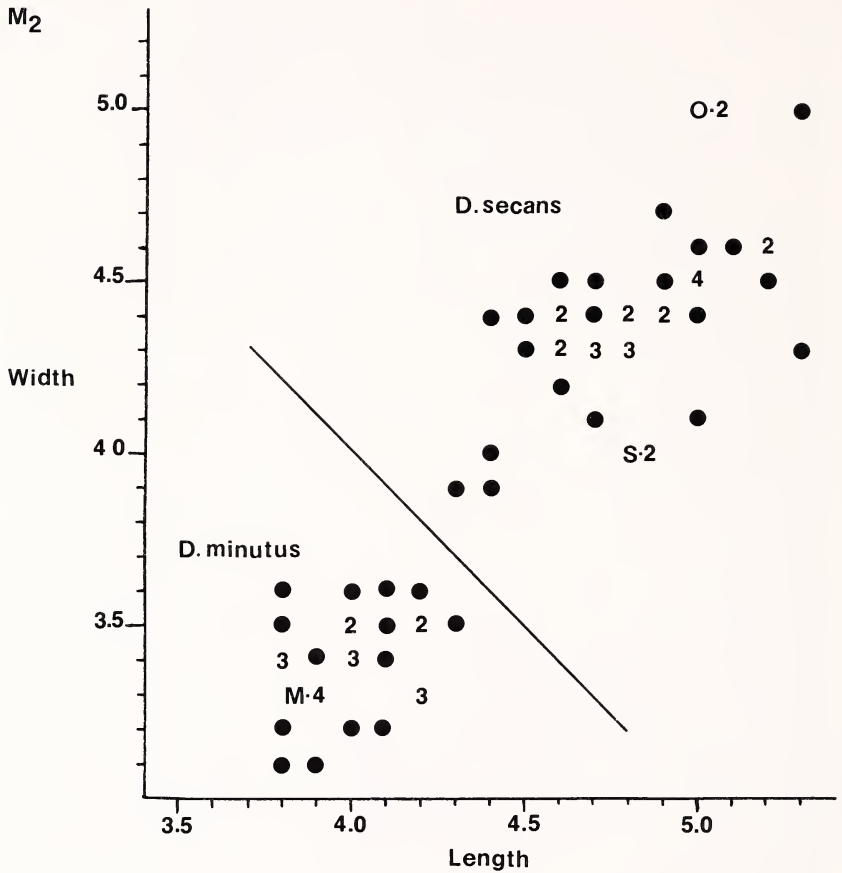


Fig. 12.—Plot of length and width of  $M_2$ s of *D. secans* and *D. minutus* from a single horizon at CM loc. 34 (Gardnerbuttean). S, holotype of *D. secans* (from AMNH loc. Wind River beds); O, holotype of *D. olseni* (CM loc. 34); M, holotype of *D. minutus* (CM loc. 34). Numbers indicate number of specimens of that size.

is derived (node 5) in larger size, greater robusticity and bunodonty, and reduction of  $P_4$  paraconid. The latter clade retains the primitive condition in lacking a postmetacristid on  $P_4-M_3$ , a talonid notch on  $M_{1-3}$  and, initially (*Wasatchia*), in having an unreduced molar paraconid directly anterior to the metaconid. The derived condition (postmetacristid on  $P_4-M_3$ ; talonid notch on  $M_{1-3}$ , with paraconid reduced and slightly medial) defines most specimens of *D. s.-metsiacus* (node 2), some of which also approach the derived morphology of *Artiodactyla* sp. A and sp. B (node 6)—elevated and conjoined paraconid

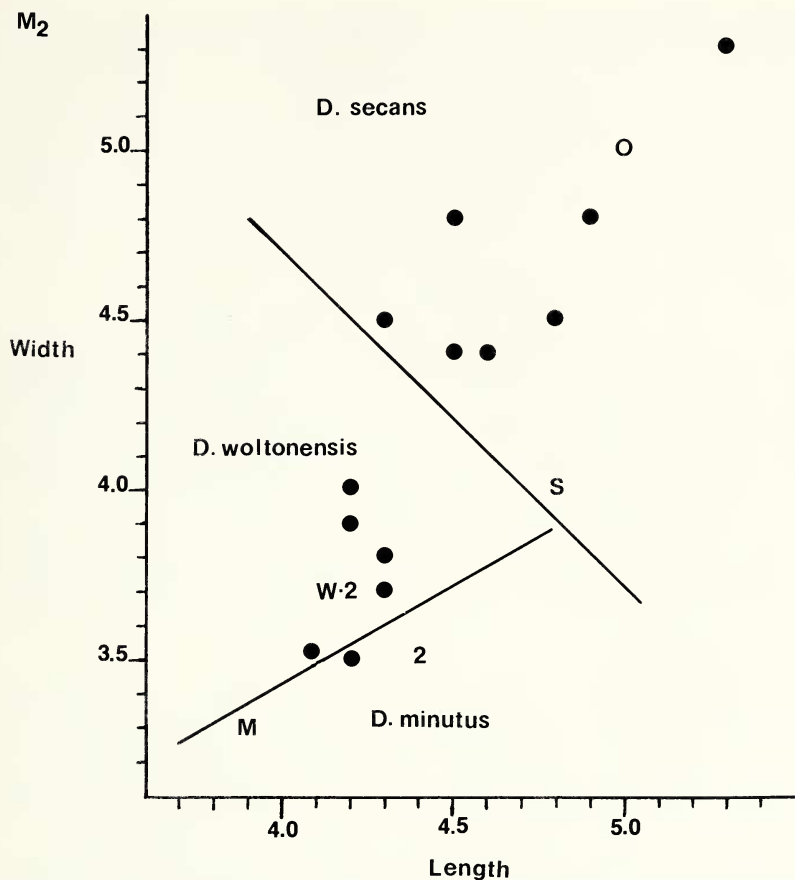


Fig. 13.—Plot of length and width of  $M_2$ s of *D. secans*, *D. minutus*, and *D. woltonensis* from Lostcabinian localities in the Wind River Basin. S, holotype of *D. secans* (from AMNH loc. Wind River beds); O, holotype of *D. olseni* (CM loc. 34, Gardnerbuttean); M, holotype of *D. minutus* (CM loc. 34, Gardnerbuttean); W, holotype of *D. woltonensis* (CM loc. 1077, Lostcabinian). Numbers indicate number of specimens of that size.

and metaconid; hypoconulid lingual, close to, but isolated from a tall entoconid, which is subequal to the hypoconid; broad postcingulid; talonid open lingually between bases of metaconid and entoconid. These features are retained and further modified in primitive antiacodontids and homacodontids (node 6A; Stucky and Krishtalka, manuscript). Also derived over the *D. s.-metsiacus* condition is *D. gracilis* (node 7), in its severely reduced and more medial paraconid on  $M_{2-3}$ , compressed trigonid on  $M_{1-3}$ , small size and more gracile cusps. *D. s.-kelleyi* and



all other diacodexeines and leptochocerids (node 3) are derived over *D. s.-metsiacus* in the greater frequency and degree of expression of an expanded molar metaconid, hypoconid and protocone, a molar talonid notch, a  $P_4$  and molar postmetacristid, elongate  $P^{3/3}$ , stronger  $P^3$  protocone, and shorter  $M_3$  hypoconulid lobe. *D. minutus*, *D. woltonensis* and *D. s.-secans* (node 4) share the most frequent presence and strongest development of a molar talonid notch and  $P_4$ - $M_3$  postmetacristid, but, as discussed above, these features may have arisen in parallel in *D. minutus* and these taxa from *D. s.-metsiacus*. *D. minutus* is derived (node 8) in its deeper talonid basin, small size, and concomitant more distinct conules, conulecristae and less inflated cusps. *D. woltonensis* and *D. s.-secans* (node 4A) are most robust, and differ from one another principally in size, with the former being most robust in proportion to its smaller size (node 9), and having a shallower talonid basin. Leptochocerids (node 10) share the major features and robusticity of *D. s.-secans* and *D. woltonensis*, but are further derived in the hypertrophy of  $P^{4/4}$  and  $M^{1/1}$ , the progressive decrease in size of the molars from  $M^{1/1}$  to  $M^{3/3}$ , and the deeper talonid basin on  $M_{1-2}$ .

These relationships, along with the known occurrence of the taxa, are depicted in a temporal framework in Fig. 11. The polarities of the shared-derived features among these taxa coincide with their stratigraphic occurrence.

The fossil record of North American artiodactyls, like that of primates, perissodactyls, rodents, insectivores, and some condylarths, is sufficiently rich and dense to reveal evolutionary tempo and mode. A measure of the latter is the kind and degree of morphological difference between sister species combined with the stratigraphic record. The particular circularity discussed in the introduction—where species determinations result *a priori* in certain evolutionary patterns and vice versa—has, we think, been avoided. The diacodexeine species recognized here are grounded in morphological distinction among lithosympatric and/or penecontemporaneous units. The evolutionary patterns emerge independently from the congruence of shared-derived features and their polarities among these species in a stratigraphic context.

Among the diacodexeines and allies treated here, the evolutionary tempo appears to have been gradual, with chronocline shifts in the degree and frequency of expression of evolving features, and their canalization within single lineages and branching taxa. As a corollary, morphologic change within these artiodactyls is mosaic—rates, patterns, and amount of change of individual features vary from incrementally continuous and slow (for example, the development of a postmetacristid and talonid notch on the lower molars of *D. secans*), to more nearly abrupt (for example, the appearance of a severely re-

duced and nearly medial paraconid on  $M_{2-3}$  of *D. gracilis*), to stasis (for example, fixation of a slightly internal molar paraconid in three lineage segments of *D. secans*). The degree of gradualism appears to be greater in lineage-species (for example, *D. secans*) and less at cladogenetic events (for example, the origins of *D. woltonensis* and *D. minutus*); the apparent difference in rates will be tested by a more dense fossil record. Microevolutionary processes can account for both cladogenesis and anagenetic change among these artiodactyls; macroevolutionary processes are not called for.

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NOTES ADDED IN PROOF.—1. In Table 7 (p. 450), the sequence of specimens UCM 52551B-52551L, 52556B, 52562B has been renumbered as UCM 52586-52598, respectively.

2. Since this paper went to press, two critical articles concerning *Diacodexis* have appeared. K. D. Rose (*J. Paleont.*, 59:1203-1226, 1985) now holds that the postcranial specializations in *Diacodexis* may not preclude its basal position within Artiodactyla, a conclusion corroborated by the dental evidence presented in this paper.

P. D. Gingerich (*Paleobiol.*, 11:27-41, 1985) contends that early Wasatchian *Diacodexis metsiacus* (= *D. secans* of this paper) exhibits evolutionary stasis, in contrast to the evidence presented here for significant morphologic anagenesis in this Wasatchian (54.5 ma)-early Bridgerian (50 ma) species-lineage. This contrast, and Gingerich's apparent stasis in *D. secans*, applies only to the  $\log L \times W$  of  $M_1$ . Size of  $M_1$  is indeed static, as we note several times in this paper. However, the  $\log L \times W$  of  $M_1$  is neither the sole morphology of *D. secans*, nor the sole indicator of evolutionary tempo. As discussed above, suites of other dental characters in *D. secans* show moderate to considerable anagenetic change.